

patches by digging holes to lay their eggs; so they asked the Shark to take the Megapodes away. This was done, but now the natives missed the Megapodes' eggs, so they asked the Shark to bring the Megapodes back but to confine them to one spot. This request was also complied with, and the result may now be seen. The Megapodes lay their eggs in two large and broad sandy spaces, and nowhere else on the island.

I suspect that there is more than a grain of true history in this legend, and that it records the fact that when the ancestors of the natives came to the island, they brought with them two main staples of their food-supply—yams and Megapodes.

35. Contributions to the Morphology of the Group Neritacea of the Aspidobranch Gastropods.—Part II. The HELICINIDÆ. By GILBERT C. BOURNE, M.A., D.Sc., F.R.S., F.Z.S.

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(Plates XXX.—XLII.*)

When, two years ago, the Society published the first part of my contributions to the morphology of the Neritacea (2), I had already accumulated a number of observations on the anatomy of the Helicinidæ, but deferred the publication of them until I was able to obtain specimens of different species from various parts of the Pacific region. Having experienced considerable difficulty in obtaining specimens sufficiently well preserved for microscopical examination, the publication of my results has been long delayed, with the result that I lose the claim to priority for several minor discoveries concerning the anatomical features of this family, for, in the meantime, Thiele (10) has given an account of the anatomy of *Hydrocena cattaroensis* in which is included a description of the female generative organs of *Helicina kubaryi*, and the following descriptions lose much of the novelty they would have possessed had they been published as soon as the facts were ascertained.

Previous to the publication of Thiele's paper, our knowledge of the anatomy of the Helicinidæ rested, for the most part, on Isenkrahe's (4) account of the anatomy of *Helicina titanica*. Isenkrahe gave a sufficiently accurate description of the external anatomy, the muscular system, the greater part of the alimentary tract, and the pulmonary cavity, but he failed altogether to distinguish the kidney, and his descriptions of the heart, the nervous system, and the reproductive organs are defective. These imperfections notwithstanding, Isenkrahe was able to confirm Troschel's opinion that *Helicina*, on account of its rhipidoglossate dentition and other anatomical characters, was closely related to the Neritidæ.

Von Jhering (5) in 1877 placed the Helicinacea and Proserpinacea

* For explanation of the Plates see pp. 806-809.

in his class Orthoneura, order Rostrifera, sub-order Rhipidoglossa, and gave a fairly accurate description, unaccompanied by a figure, of the nervous system of *Helicina* (*Sturanya* Wagner) *beryllina* Gld. E. L. Bouvier (3), in his great work on the nervous system of Prosobranch Gastropods, gave a very complete account of the nervous system of *H. sagraiana* d'Orb. and *H. brasiliensis* Gray, laying stress on its close resemblance to the nervous system of the Neritidæ, and in addition he made some further observations on the general anatomy, partly confirming and partly correcting and adding to Isenkrahe's descriptions. In 1902 Thiele (9) described the male generative organs of *Helicina japonica*, and last year he gave a description with a diagram of the female organs of *H. kubaryi*, in addition to a succinct but sufficiently exhaustive account of the general anatomy of *Hydrocena cattaroensis*.

The geographical distribution of the Helicinidæ, as is well known, presents several interesting and difficult problems. By far the greater number of species are insular and confined to the tropics. Such species as are found on continents are for the most part limited to regions near the coast, very few being known to occur any considerable distance inland. No Helicinidæ are recorded from Africa. In Europe the group is represented only by the genus *Hydrocena* from the Dalmatian coast, and this genus, as Thiele's recent work has shown, differs in several important anatomical characters from *Helicina* and its more closely allied genera. *Georissa*, a subgenus of *Proserpina*, is the only representative of the group in India, and no Helicinidæ have as yet been recorded from Ceylon. The number of genera and species reaches its maximum in the Antilles. The genus *Helicina*, as restricted by Wagner, is fairly abundant in Mexico and the Central American republics, and extends northwards into Texas and Florida, southwards into Ecuador and Peru on the west coast and to the south of Brazil on the east coast of S. America. Few species, however, are recorded from the Pacific coast of S. America, but, notwithstanding their comparative rarity on these shores, the group reappears in great abundance in the Pacific islands, extending as far east as the Marquesas and Paumotu Islands, and having many representatives in the Society, Samoan, Friendly and Fiji Islands, and in the New Hebrides and New Caledonia. Several species occur on the east coast of Australia, and some few are recorded from New Guinea, Celebes, Borneo, and Sumatra; none, so far as I can ascertain, from Java. But in this part of the world the Helicinidæ attain their maximum in the Philippine Islands, which are only second to the Antilles in the number of species. From thence the group extends north, beyond the tropical zone, to the Bonin Islands and Japan. A few species are found beyond the south-east coast of China and Siam, others again in the Malay Peninsula and Burma. Several species are found in the Andaman and Nicobar Islands, but the group is very poorly represented in the Indian Ocean. *Aphanoconia* (*Helicina*) *theobaldiana* G. & H. Nevill is recorded from the

Seychelles, and *Pseudotrochatella undulata* Morelet is a subfossil form from Mauritius. None is known from Madagascar.

In a recent work of great value to the student of geographical distribution A. J. Wagner (12) has revised the family Helicinidæ, and, founding his diagnoses chiefly on the characters of the operculum, has broken up the old genus *Helicina* into no less than thirteen genera, reserving Lamarck's appellation for the American and Antillean forms which conform to the original definition of the genus. Of the remainder I mention the largest genera. *Sulfurina* has its centre in the Philippines and extends thence to the Andamans, Nicobars, Moluccas, New Guinea, and Tahiti. *Aphanoconia*, which also seems to be centred in the Philippines, extends widely, to Japan, S. China, the Malay Archipelago, the Andamans, Nicobars, Seychelles, Moluccas, and through Micronesia and Melanesia to the Paumotu and Sandwich Islands. *Sturanya* has its centre in Fiji and Tonga, and extends thence to the Carolines, Sandwich, Society, Hervey, and Solomon Islands. *Orobophana* is found in Queensland and N.S. Wales and extends through nearly the whole of Polynesia. *Palæohelicina*, with its subgenus *Ceratopoma*, is again a Philippine genus, and extends to New Guinea, the Bismarck Archipelago, the Solomon, Louisiade and Pelew Islands. The last-named genus is, according to Wagner, closely allied to *Helicina* sensu restricto. Again, the subgenus *Retorquata* of *Helicina*, which occurs in Mexico and Central America with outliers in Florida and Texas, affords, according to the same author, a transition to such a characteristic Antillean genus as *Alcaldia*. A consideration of these statements leads to the conclusion that the Helicinidæ are capable, by what means we know not, of wide dispersal across seas and oceans, and find conditions most suitable to their existence in proximity to the sea. They appear to have originated in Mexico and Central America, and to have spread eastwards to the Antilles, where they found the conditions specially suitable, and have been differentiated into several genera (*Alcaldia*, *Lucidella*, *Eutrochatella*, *Priotrochatella*, *Proserpina*) and numerous species, and one species (*H. substriata convexa* Pf.) has found its way to the Bermudas. Others have extended down the eastern coast of S. America, but the Atlantic Ocean has proved an impassable barrier to their further extension eastward. On the Pacific side the group has been transported by some means unknown to us to the Pacific Islands, and it would appear from the evidence that it did not at first effect a lodgment in the more eastern islands, but in the Philippines, from which centre it has spread in all directions—eastward throughout Polynesia and to the Sandwich Islands, southward to New Guinea and Australia, northward to Japan and China, westward through the Dutch Indies and Malaya to the Andaman and Nicobar Islands. Very few have traversed the Indian Ocean to reach the Seychelles and Mauritius.

Very little is known of the geological history of the group. *Helicina* occurs in the post-Pliocene of N. America, but the

ancestral forms must have lived at a much earlier period, for *Proserpina* is recorded from the Eocene of the Isle of Wight, and, according to Kobelt (6), shells referable to the same genus have been found along with *Helix*, *Planorbis*, *Valvata*, and three species of *Veritina* in the Lias of Somerset. There is some reason for suspecting the correctness of the identifications in the last case, and I am unable to find any corroborative evidence of the occurrence of *Proserpina* in the Eocene, but the distribution of the Hydrocenidæ points to a geological history reaching well back into Tertiary times. *Dawsoniella* from the Carboniferous of Illinois has been attributed to the Helicinidæ, but I have already, in the first section of this memoir, discussed the affinities of this genus and pointed out that it must be a case of convergence.

However this may be, palæontology throws very little light on the origin and distribution of existing Helicinidæ, and when I began this work I hoped, not only to give a full description of the anatomy of a typical member of the family, but also, by the comparison of the anatomy of Pacific and West Indian forms, to discover some clue to the distribution of the group with its two main centres in the Antilles and the Philippines. In this, as will appear, I have been disappointed. From whatever part of the world they may come, the anatomy of the different species and even genera of Helicinidæ is so closely similar that it is hard to find any difference between them. It is true that I have not been able to procure many species of Pacific Helicinidæ, but I have examined fairly well preserved specimens of *Orobophana*, *Aphanoconia*, and *Paleohelicina*, and these three genera may be taken as typical of the more widely distributed Pacific forms.

The material at my disposal was as follows:—

I. Antillean forms.

- Alcudia palliata* Ads. Contrivence, Walderston, Jamaica.
Alcudia hollandi Ads. Swing Hill, Walderston, Jamaica.
Lucidella aureola Fér. Bog Walk, Spanish Town, Jamaica.
Eutrochatella pulchella Gray. Bog Walk, Spanish Town,
 Jamaica.

The above were kindly collected for me and preserved in Perenyi's fluid by Mrs. G. B. Longstaff, F.L.S.

II. Pacific, Australian, and Indian forms.

- Aphanoconia gouldiana* Forbes, from Torres Straits: for specimens of this species I am again indebted to Mrs. Longstaff, who procured them for me from Mr. C. Hedley, of the N.S. Wales Museum.
Aphanoconia andamanica Benson.
Aphanoconia merquiensis Pfeiffer.
Aphanoconia rogersii, sp. n.

These three species are from the British Museum and formed part of the collection made in the Andaman Islands by Mr. G. Rogers.

They were numbered respectively 16, 30, and 31. The first two I have identified without difficulty, the third appears to be new to science, and I will give a diagnosis of it in the latter part of this paper. I am indebted to Mr. E. A. Smith for these and for the two following species:—

Orobophana pachystoma ponsonbyi Smith. Admiralty Islands.
Palceohelicina idæ Wagn. Amboina.

In describing the anatomy it will be convenient to take *Alcadia* as the type, and to note such differences as may exist between it and the other genera at the end of the description of each system of organs.

*External Characters, Mantle, Mantle-cavity,
and Muscular System.*

Isenkrahe (4) has given an account of these so sufficient and accurate that it is not necessary for me to do more than call attention to some special features exhibited in fig. 1 (Pl. XXX.), which is a representation of a left side view of *Alcadia palliata*: the mantle has been cut through on the left side close above the columellar muscle, the cut has been extended back to nearly the extreme hinder end of the mantle-cavity, and the mantle has been turned over towards the right. As compared with the *Neritidæ*, in this and in all the other species of *Helicinidæ* that I have examined the foot is attached to the head and body by a longer and narrower pedicle, the opercular lobe is relatively smaller, the snout is narrower and longer, the columellar muscles of greater antero-posterior length, and the whole body is longer, giving the appearance of an increase in the coiling of the visceral mass, but this last feature is more apparent than real, as I shall show. A glance at the figure shows that the increased length of the body is chiefly due to the elongation of the post-tentacular region and the part of the body immediately following. Using Amaudrut's (1) phrases, we have an almost extreme case of "allongement posttentaculaire," followed by an "allongement dorsal," and many of the peculiar features of helicimid anatomy are to be explained by the excessive growth in length of these two regions. The post-tentacular region lies above the anterior two-thirds of the columellar muscle, and its posterior limit is marked by two or three deep wrinkles of the body-wall. The body-wall of this post-tentacular region is fairly stout and muscular, and the epidermis is, as a rule, deeply pigmented. The colour differs in different species. It is nearly black in *Alcadia*, grey shading posteriorly into white in *Eutrochatella pulchella*, yellowish grey in *Lucidella aureola*, a dark chocolate-brown in *Palceohelicina idæ*, and a bright chestnut-brown in *Aphanoconia gouldiana*. In the post-tentacular region are contained the buccal bulb and the greater part of the œsophageal pouches. In the dorsal region following on the post-tentacular the body-wall is thin and nearly

transparent, the musculature is feeble, and the epidermis is not pigmented. This dorsal region is relatively of considerable length; its concave lower border corresponds very closely in length with the surface of insertion of the left columellar muscle; its upper surface extends back to the pericardium. It contains nearly all the coils of the intestine, the œsophagus, the radular sac, and the hinder lobes of the œsophageal pouches. Its roof forms the floor of the hinder part of the mantle-cavity. In consequence of the elongation of these two regions, but particularly of the dorsal region, the mantle-cavity is continued very far back; so far that, measured from its most anterior to its most posterior limit, it makes nearly a complete turn of a spiral, whereas in *Neritina* and *Neritina* it makes little more than half a turn. Broad in front where its roof passes from the right to the left columellar muscle, the mantle-cavity becomes narrower and narrower posteriorly and ends in a pointed *cul-de-sac* below and somewhat to the right of the lower surface of the visceral mass. Its extreme posterior limit is not quite visible in fig. 1. With the hinder end of the mantle-cavity the pericardium has also been carried very far back. It is laid open in fig. 1 to show the position of the heart. It will be seen that the single auricle seems to lie behind the ventricle, and not in front of it as does the larger left auricle in the *Neritidæ*. In horizontal sections, such as those depicted on Pl. XXXIII. figs. 18 and 19, this posterior position of the auricle forces itself so much upon one's attention that I was led to form the theory that the single auricle of the *Helicinidæ* corresponds not to the left and larger, but to the right and rudimentary auricle of the *Neritidæ*; and in my memoir on the morphology of the latter family (2, p. 833) I prematurely gave expression to this view, which seemed to me the more probable because I found that in correlation with an increase of the pallial vessels in *Septaria* the right auricle became relatively larger and took an obviously larger share in carrying blood from the pallial vessels to the ventricle. But since then, after a careful study of the relative positions of the kidney, the uropore, the rectum, and the heart in the *Helicinidæ*, I have satisfied myself that this view was erroneous.

As a consequence of the dorsal elongation of the body all these organs have been rotated through an angle of rather more than 90° , in such wise that the pyloric end of the stomach, which in the *Neritidæ* is directed forward and to the left, comes to lie at the right posterior end of the body in the *Helicinidæ*, and the swollen œsophageal end of the stomach, which is posterior and somewhat to the left in the *Neritidæ*, is directed anteriorly and to the right in the *Helicinidæ*, forming a conspicuous rounded prominence at the extreme end of the visceral mass (Pl. XXX. fig. 1, *St.*). To understand the nature of this rotatory movement the reader should refer to fig. 42 of my memoir on the *Neritidæ*. This figure represents a horizontal section of *Paranerita gagates*, and shows the position of the œsophageal (*St.*) and pyloric (*St.*) divisions of the stomach. It should be noticed

that the extremity of the visceral mass, lying to the right, is wholly occupied by the liver and gonads. If, now, the reader will lay a tobacco-pipe in front of him on the table, the bowl (representing the œsophageal division of the stomach) to his right, the stem (representing the pyloric division of the stomach) to his left front, it will occupy much the same position as does the stomach in the figure referred to. If, while the bowl is kept pressed against the same spot on the table, the stem is lifted up and rotated through an angle of rather more than 90° till it points over the observer's right shoulder, the whole pipe will have been rotated through an angle which brings it into the position of the stomach of the Helicinidæ—the animal being supposed to be placed foot downwards upon the table with its head turned away from the observer. As all the organs of the left side of the body, including the posterior end of the mantle-cavity, the pericardium, the heart, the kidney, and the coils of the intestine, have shared in this movement of the pyloric end of the stomach, their positions have been nearly completely reversed, and the left auricle instead of lying in front of the ventricle has come to lie behind. The right auricle has entirely disappeared in the Helicinidæ, and the rectum, having undergone some degree of displacement in connection with the above-described movement of rotation, is no longer enveloped by the ventricle.

The kidney has also undergone a curious and at first sight a puzzling change of position. In the Neritidæ, as described in my previous memoir (2, see Pl. XLVI. fig. 1 for its position in *Septaria*, Pl. LIV. fig. 29 for its position in *Paranerita gagates*), its glandular part lies to the left hand of and partly below the rectum: posteriorly the glandular part opens into the spacious non-glandular bladder or ureter, and the latter runs forward, below the glandular part, to open by the uropore into the mantle-cavity on the right of and close to the base of the ctenidium. In this family the greater part of the kidney lies in the roof of the mantle; it is only its posterior extremity that passes below the rectum and invades the visceral mass, where it lies just above the pyloric end of the stomach. The effect of the rotation of the last-named organ in the Helicinidæ is that the kidney has been carried round till it comes to lie wholly in the visceral mass, on the lower side of the latter, between the loop of the rectum which passes round this region and the pyloric division of the stomach, as may be seen in the series of sections (Pl. XXXIII. figs. 17 to 20) and in the diagram (Pl. XXXIV. fig. 24), which is a reconstruction from this series of sections. The kidney, in short, has been turned completely round, so that its originally posterior end looks to the left front and the uropore opens into the right hinder corner of the mantle-cavity, the reno-pericardial canal, maintaining its relation to the uropore, into the right posterior corner of the pericardium. It is further to be observed that the visceral mass, though apparently more coiled, is really less coiled in the Helicinidæ than in the Neritidæ. In all systematic works stress

is laid on the fact that the internal partitions of the shell are absorbed in both these families. This absorption has not proceeded quite so far in the Neritidæ as in the Helicinidæ. In *Nerita* and *Paranerita* there is a recess in the upper right-hand part of the shell which contains that lobe of the visceral mass which consists wholly of liver and gonads and represents the visceral spire of other Gastropods. This recess and the lobe of the visceral sac corresponding to it are not found in the Helicinidæ: the wall of the œsophageal division of the stomach comes very near to the surface (Pl. XXXIII. figs. 17 & 18), and the liver and gonads are disposed at the sides of and above the pyloric division of the stomach. The more coiled appearance of the whole is due to the elongation of the post-tentacular and dorsal regions, not to the retention of a larger section of the visceral spire of the presumed gastropod ancestor than in the Neritidæ.

From what precedes, it follows that most of the peculiarities of the Helicinid organization are the result of excessive growth and elongation of a particular region of the body, and it is an interesting confirmation of the correctness of the above account of the manner in which the Helicinid organization has been derived from the Neritid that, if one makes a plasticine model of the stomach, kidney, rectum, and intestinal coils as they occur in *Paranerita*, and then rotates the stomach in the manner described, the intestinal coils assume very nearly the position found, with more or less variation in detail, in all Helicinids.

After this general explanation of the mutual relations of the principal visceral organs in the Helicinidæ, I need only refer to particular features in the several systems of organs which I have to describe in detail. Before proceeding, it should be put on record that there is not a rudiment of the ctenidium in the Helicinidæ, and I cannot even find a trace of an osphradium. The cephalic penis, characteristic of the males of the Neritidæ, is also absent, and there is no external difference between the males and females in any of the species that I have examined.

The Alimentary Tract.

The complex of organs formed by the buccal cavity, the pharynx, the œsophagus with its smaller and larger glandular annexes, the radula, the radular sac, and the odontophoral cartilages and their muscles, can only be studied by dissection, and this is by no means an easy task in animals so small as most species of Helicinidæ are. The relations of the various organs to one another are far too complicated to trace out in sections. The following description applies chiefly to *Alcadia palliata* and *A. hollandi*, but will serve almost equally well for any of the other species that I examined, for all are very much alike except for the details of the radular teeth.

The mouth is a gaping circular orifice, situated at the extremity of the downturned snout: it is surrounded by folded muscular lips.

The buccal cavity occupies the snout, in front of the tentacles. It is a simple funnel-shaped cavity bounded by a rather thick muscular wall, the internal surface of which is thrown into about 19 or 20 longitudinal folds. The cavity is lined by a layer of rather long columnar epithelial cells which secrete a thick cuticle. Dorsally the buccal cavity is prolonged backward into a little glandular diverticulum which lies above the median part of the cerebral commissure. The buccal cavity is separated from the pharynx by a constriction, deepest on the dorsal side, where the cerebral commissure lies in it. In a surface view, before disturbance of the various parts, this constriction is not visible from above, as it is covered over by the anterior salivary glands shortly to be described, and muscle-fibres pass from the walls of these glands to the walls of the buccal cavity and of the snout. Consequently the cerebral commissure seems to be embedded in the buccal mass.

The passage from the buccal cavity to the pharynx is narrow. The pharynx is a relatively spacious sac, of which the cavity is continued posteriorly into the œsophagus above and into the radular sac below. Beneath and at the sides of the anterior end of the radular sac lie the odontophoral cartilages, the anterior ends of which project forward into and occupy the greater part of the lower moiety of the pharyngeal cavity. It will readily be understood that, in consequence of the projection of the anterior ends of the odontophoral cartilages into the pharyngeal cavity, the latter extends round them both at the sides and below. Below the cartilages the pharyngeal extension forms a broad flattened diverticulum, reaching back nearly to the posterior ends of the anterior cartilages, as far as the point marked *x* in fig. 3 (Pl. XXX.). Laterally, the line of attachment of the pharyngeal wall to the anterior odontophoral cartilages is roughly indicated in the same figure by the curved line running upward and forward from the point *x* towards the opening of the œsophagus. It results from this arrangement that in an oblique section, such as is represented in fig. 4 (Pl. XXX.), the pharynx appears to give off two posterior diverticula, lying outside the anterior ends of the odontophoral cartilages. The inner walls of these diverticula are thin and composed of a single layer of cubical epithelial cells: they are continued round the anterior and upper edges of the cartilages into the lining membrane of the radular sac. The outer wall of each diverticulum is strengthened by a thin plate of cartilage, too small and transparent to be recognized in dissection, but readily recognizable in sections. These lateral pharyngeal cartilages serve for the attachment of muscles, one set of which run forward to be inserted on the walls of the snout, the other set run backward and are inserted on the odontophoral cartilages; the former are protractors, the latter retractors, of the walls of the pharynx.

A portion of the epithelial lining of the outer wall of each

diverticulum is composed of very long attenuated epithelial cells, among which are long club-shaped glandular cells. This glandular strip may be traced upward and forward to the thickened lip of the œsophageal opening, where it forms a prominent ridge which passes above into the anterior pair of salivary glands, to be described shortly.

As is shown in Pl. XXX. fig. 2 and in the section drawn in fig. 4, the radular sac opens into the pharynx by a widely gaping aperture situated in the trough-shaped depression between the anterior ends of the anterior odontophoral cartilages. Posteriorly the radular sac passes between the posterior odontophoral cartilages and runs at first to the right of and below the œsophagus, but soon mounts upwards and to the left, the two organs, œsophagus and radular sac, being twisted round one another as shown in fig. 2. The radular sac is short in *Alcadia palliata* and is of no great length in any of the species that I have studied. The greater or less length of the radular sac appears to be an individual rather than a specific character. The characters of the radular teeth will be dealt with in a separate section.

The odontophoral cartilages were described in some detail by Isenkrahe for *Helicina titanica*, and I have but little to add to his account. A ventral view of these structures in *Alcadia palliata* is given in Pl. XXXI. fig. 5, and a sketch of a dorsal view of the same structures in *Eutrochatella pulchella* in fig. 6: both figures are drawn to the same scale. As may be seen from the specimens figured, the odontophoral cartilages exhibit specific differences in relative size and proportion, but these differences are of too slight and elusive a character to be expressed in a description, and scarcely important enough to make it worth while to give a separate figure for each species examined. The essential structure is the same in all. There are two pairs of cartilages, an anterior and a posterior. Each member of the anterior pair is a plate having the form of a more or less elongated isosceles triangle; the margins of the plate are thickened and rounded, the central portion remains thin. The plate is bent in such a way that its lower margin is bent inward posteriorly and its upper margin outward. The posterior margin or base of the triangle, forming the articular surface for the posterior cartilage, runs obliquely from above downwards and inwards. The lower margins of the two cartilages are connected by a tough fibrous band, and their thickened edges serve for the attachment of the intrinsic and extrinsic odontophoral muscles. The posterior cartilages are short conical masses; their apices directed backwards; their ventral surfaces convex and their dorsal surfaces more or less concave. Their broad anterior ends are shaped to correspond with the articular surfaces of the anterior cartilages, and the two are firmly held together by muscular fibres, whose arrangement is indicated in fig. 5. It follows from the above description that the odontophoral cartilages form the sloping sides of a V-shaped trough, the concavity of which looks upwards and supports the

anterior part of the broad radular ribbon. The median and admedian radular teeth lie in the floor of this trough, the great lateral teeth lie in the angles between its floor and sides, and the uncini form curved rows running upwards and backwards along its sloping sides. The radular ribbon is attached by strong muscular bands to the cartilages. These muscles run obliquely forwards from the radula to be attached to the anterior cartilage of either side, and obliquely backwards to be attached to the posterior cartilages, these two sets of muscles causing the ribbon to slide forward and backward over the smooth surfaces of the cartilages.

The relation of the œsophagus to the radular sac and odontophore is shown in fig. 3, which is a drawing of a dissection of these structures in *Alcadia palliata*. The left œsophageal pouch and the left side of the œsophagus have been cut away, and the roof of the œsophagus has been lifted back to the right side to show the entrance to the right œsophageal pouch and other structures. In the angle of the deep fold between the œsophagus and radular sac are seen the buccal ganglia (*g.buc.*) lying just above the middle of the anterior odontophoral cartilages. The opening of the œsophagus into the pharynx, situated just in front of and above the buccal ganglia, is irregularly funnel-shaped, with thickened and folded lips projecting forward into the pharyngeal cavity. Laterally, these lips are deeply grooved, and on either side the groove is continued backward and downward into the lateral pharyngeal diverticulum described above, and upward and somewhat forward into the anterior salivary gland of its own side. These anterior salivary glands are formed by a pair of pocket-like forward projections of the œsophagus, which in their natural position lie side by side and form a pair of pouches lying above the cerebral commissure. Between them is an anterior cœcal diverticulum continuous behind with the median dorsal groove of the anterior part of the œsophagus. When separated by an incision in the mid-dorsal line and turned outwards, the anterior salivary glands present the appearance shown in fig. 2. Internally their walls are raised into a number of thick glandular ridges: the outermost of these ridges is specially thick and is continued downward, in the groove passing to the side of the œsophageal orifice, into the glandular ridge on the outer wall of the pharyngeal diverticulum, as has been described above.

The anterior section of the œsophagus, lying above the odontophore, is fairly wide. Internally, its walls present a number of longitudinal glandular ridges, and in the mid-dorsal line there is a deep groove bounded internally by prominent ridges; posteriorly this groove shallows and eventually dies out. On either side of this anterior section of the œsophagus is a gaping oval orifice (figs. 2 & 3, *o.a.p.*) leading into the large œsophageal pouches, or, as some would call them, the posterior salivary glands. The last-named structures are capacious irregularly lobulated sacs with large cavities. Their inner walls are

lined throughout by a glandular epithelium, consisting, as far as I was able to determine, almost wholly of very long goblet-shaped secretory cells containing zymogen granules, with very few attenuated supporting cells lying between. The histological characters of the epithelium were not, however, very well preserved in any of my specimens. The two pouches are closely pressed against the sides of the œsophagus, and in the species in which they are longest follow the turns of the latter. Hence, as the œsophagus makes a turn towards the left before it passes down through the loop of the rectum, the right œsophageal pouch generally passes over to the left side and above the œsophagus, the left pouch passing to the right and below the œsophagus and radular sac. The œsophageal pouches are relatively short in *Alcedia palliata* and of approximately equal width throughout, but they are much longer and diminish in diameter towards their posterior extremities in *A. hollandi*. They are particularly long and of a deep chocolate colour in *Palæohelicina ida*; in most species they are white in spirit-specimens.

Behind the openings of the œsophageal pouches the œsophagus narrows somewhat abruptly in diameter; the glandular internal longitudinal ridges disappear, and are replaced by nine or ten longitudinal ridges formed by columnar ciliated epithelial cells, and these may be traced throughout its course to the stomach. This course is a long one, for the stomach lies aslant on the lower side of the visceral mass, below the greater part of the lobes of the liver and below the coils of the intestine. As seen from above and behind, it is a large pyriform sac, the narrower end lying just above the posterior corner of the pericardium; the broader end forming on the right side of the visceral mass a large rounded prominence which fits into the concavity on the ventral side of the right columellar muscle. The œsophagus enters the stomach on the upper side of its broader end, and its course in the several species examined will be best understood by reference to Pl. XXXII. figs. 10 to 15. Passing to the left as it enters the visceral mass, the œsophagus lies above the first coils of the rectum, then passes below the recurrent coil of the rectum, and so arriving at the dorsal surface of the stomach runs along the latter as a flattened tube and opens, as stated above, into its broader end, dilating considerably just at its point of entrance. This dilatation, which might almost be described as a diverticulum of the stomach itself, receives right and left the wide ducts of the liver (Pl. XXXI. fig. 7, and Pl. XXXII. fig. 16, *l.d.*).

The internal structure of the stomach is very complicated. It attracted the attention of Isenkrahe, who gave a fairly accurate description of it. Fig. 7 is a representation of a dissection of the stomach made from behind and below the visceral mass. The œsophagus is shown at *æ.*, and its entrance into the stomach is indicated by the arrow. The entrance of the left liver-duct is shown at *l.d.*; that of the right liver-duct lies on the far side of the prominent curved ridge guarding the entrance to the

œsophagus. Both the œsophageal aperture and those of the liver-ducts are surrounded by complicated epithelial ridges, which, as shown in the drawing, converge towards and pass into a deep groove running along the dorsal side of the narrower pyloric moiety of the stomach. The edges of this groove are bounded by two prominent folds; that on the right side (the left in the drawing) being continued towards the œsophageal opening as a projecting ridge, ending at the side of the aperture in a very prominent crescentic projection covered by a thick iridescent cuticle.

The internal surface of the stomach is lined by a mixed glandular and ciliated columnar epithelium, the characters of which are shown in Pl. XXXI. fig. 8; the glandular elements predominate in the œsophageal, the ciliated elements in the pyloric, moiety of the stomach. The epithelial cells are lower in the furrows, taller and more slender in the ridges, these latter structures being formed entirely by thickenings of the epithelium, and not by foldings of the wall of the stomach. The crescentic projection to the right of the œsophageal opening is formed by a local modification of the epithelium, the cells of which are here extraordinarily long, with nuclei placed about the middle of their length, and with apparently homogeneous transparent cytoplasmic contents (Pl. XXXI. fig. 9); they are all of one kind, without any admixture of glandular cells, and, so far as one can judge, they are not themselves glandular. The free ends of these cells are covered by a very thick and tough cuticular coat, which stains deeply in hæmatoxylin, brazilin, and other ordinary dyes. The whole structure corresponds to the "flèche tricuspidé," of which the characters have been thoroughly described for Lamellibranch stomachs, and which has been noted as occurring in several Gastropod stomachs. There is no definite crystalline style in Helicinidæ, but in several specimens that I dissected I found the cavity of the stomach filled by a semitransparent gelatinous mass, which appeared to be similar in origin and composition to a crystalline style. In several specimens I found that the intestinal end of the groove of the pyloric moiety of the stomach was occupied by closely compacted faecal pellets or rods, while the cavity below was filled either by the gelatinous mass above mentioned or by a loose mass of semi-digested food. It may be inferred from this that digestion is effected in the general cavity of the stomach, and that the indigestible materials of the food are collected into the dorsal groove and passed into the intestine.

Morphologically, the stomach of the Helicinidæ closely resembles that of the Neritidæ, and further bears a resemblance to the stomachs of the Fissurellidæ and Scissurellidæ, which, as in this case, have a groove leading from the hepatic ducts towards the intestinal end of the stomach, but no spiral cæcum.

The small intestine is a comparatively narrow tube, which after leaving the pyloric end of the stomach runs back for a short distance over the dorsal surface of the latter, parallel with the

oesophagus, and then turning upwards and forwards describes one or more convolutions before it passes into the large intestine. The small intestine can always be distinguished by its white colour and narrow diameter; it varies considerably in length in different species, being longest in *Alcadia palliata* and *Orobophana ponsonbyi*, shortest in *Eutrochatella pulchella*. Internally it is lined by a columnar ciliated epithelium containing a few gland-cells, and its internal surface is increased by a well-marked internal ridge or typhlosole formed by long ciliated cells. The small intestine passes abruptly into the large intestine, the latter being of much larger diameter and having pigmented walls. In all species of *Alcadia* and *Helicina* examined, the large intestine runs forward and to the left below the oesophagus, then bends abruptly back, forms a wide circular loop which passes above the oesophagus, in front of the anterior end of the stomach and along the inner wall of the anterior end of the pericardial cavity: it then turns downwards and to the right, passes right round the lower side of the stomach, and mounting upwards again behind it runs in the right side of the roof of the mantle-cavity to open by the anus, opposite the right tentacle. In the first part of its course, *i. e.* in the short length between the small intestine and the recurrent circular loop, the large intestine is lined by very evenly disposed columnar ciliated cells, among which I could not detect any gland-cells, and this part of the intestine is not, as a rule, full of faecal matter. This section of the intestine may be described as the large intestine proper, to distinguish it from the rectum, into which, however, it passes without any obvious line of demarcation. The rectum is always full of faecal debris, and its epithelium consists of (1) columnar ciliated cells; (2) goblet-shaped gland-cells filled with coarse granules which stain deeply in hæmatoxylin and are therefore probably mucinogenous; (3) smaller gland-cells containing small yellow granules. There is no typhlosole either in the large intestine or the rectum.

Noticing that the coils of the gut differed in the different species, I have been at some pains to work out this character in detail, and figs. 10 to 15 (Pl. XXXII.) show the coils characteristic of six different species. An examination of the figures will give a better idea of the differences than any description. It will be noticed that there are three main types. In *Alcadia palliata*, *A. hollandi*, *Orobophana ponsonbyi*, and *Palæohelicina* the intestinal coils, though differing in detail, are alike in this respect, that the small intestine runs back more or less parallel to the oesophagus over the dorsal surface of the stomach, and the large intestine makes a bend to the right below the oesophagus and then, turning back on itself, makes a second bend to the right above the oesophagus. The second type of arrangement is shown in *Lucidella aureola* (fig. 14). In this species the oesophagus is not pressed against the dorsal surface of the stomach, but runs obliquely down to it; the small intestine passes forward from the pyloric end of the stomach, crosses over

the œsophagus, and curves round it till it nearly touches the pyloric end of the stomach again; here it passes into the large intestine, which turns sharply back, passes round the œsophagus again, and coming to the surface sweeps round to the left in front of the anterior corner of the pericardium to form the descending loop of the rectum. This type is easily derived from the first by the shortening of both the small and the large intestine, in consequence of which the former is hooked round the œsophagus and one of the bends characteristic of the first type is suppressed. The third type, seen in *Eutrochatella pulchella* (fig. 15), differs considerably from the other two. The small intestine is even shorter than in *Lucidella*, and the loop formed by the large intestine and the first section of the rectum lies wholly on the dorsal side of the œsophagus; this condition is clearly due to the gut being much shorter than in the other types, and it appears to be quite a constant feature in *Eutrochatella*. The intestinal coils of *Aphanoconia andamanica* are singularly like those of *Eutrochatella*.

I may appear to be giving an undue amount of attention to characters of no obvious morphological or physiological importance, but it is just because they may be claimed to be of importance in the economy of the species that I have spent a considerable amount of time in working out these details. Each species seems to have a characteristic arrangement of the coils of the intestine, and the arrangement is remarkably constant in individuals of the same species, allowance being made for displacements due to the greater or less state of contraction of the specimens. Closely allied species, such as *Alcadia palliata* and *A. hollandi*, have a very similar arrangement, yet sufficiently different to allow one to recognize them at a glance after obtaining some familiarity with their anatomy. *Lucidella* and *Eutrochatella*, both separated from *Alcadia* and from one another by distinctive characters of shell, operculum, and radula, differ in a nearly corresponding degree in the coils of the intestine. *Orobophana* and *Paleohelicina* are Pacific forms which must have been derived from American *Helicine*, the latter being closely related to *Alcadia*, and they resemble the last named in the coils of the intestine. To this extent it may be claimed that two, three, or more characters vary together in these genera; but *Aphanoconia* presents a difficulty, for this genus is far removed from *Eutrochatella* in shell and radular characters, and is in these respects closely related to *Paleohelicina*, yet its intestine is as nearly as may be that of an *Eutrochatella*. As the two genera cannot possibly stand in close genetic relationship to one another, the similarity in the pattern of the intestinal coils must be due to parallelism, similar causes producing similar deviations from type in the two organisms. It has been shown that the differences in pattern are attributable to differences in the length of the large and small intestines, and this is probably connected with different forms of food. As we are ignorant of

the habits of the various species of Helicinidæ, and do not even know for certain whether each or any species is restricted to a particular kind of food, it would be rash to speculate on this question, but such evidence as I have collected does seem to show that such apparently trivial characters as the coils of the intestine are of some physiological importance, and are therefore subject to the action of natural selection.

The Cœlom.

The cœlom is represented by the pericardial cavity, which, although it is of much smaller extent and less complicated than in the Neritidæ, is nevertheless a cavity of relatively considerable size, as may be seen by an inspection of figs. 17 to 20 (Pl. XXXIII.). As is shown in fig. 1 (Pl. XXX.) it comes close to the surface of the left side of the visceral mass, and extends forwards nearly as far as the posterior end of the left columellar muscle and backwards round the lower side of the visceral mass as far as the end of the mantle-cavity. It is bounded externally by the very thin body-wall, posteriorly by the inner wall of the mantle-cavity, internally by the kidney (figs. 17 to 20). At about the middle of its length it is a cavity of considerable depth, extending some way into the visceral mass below the pyloric division of the stomach. The reno-pericardial canal, which will be described in connection with the kidney, opens into its right posterior wall, at some little distance from its hindermost end (fig. 19); otherwise it is a closed sac containing the auricle and ventricle of the heart, and does not require further description.

The Hæmocœle, Circulatory and Respiratory Systems.

The blood-vascular system, as in all Molluscs, consists partly of large lacunar spaces, which collectively are known as hæmocœle, and partly of vessels with definite walls. The hæmocœlic spaces surround the viscera, and there is a specially large lacunar space below the buccal bulb, in which lie the pleuro-pedal ganglia. In the visceral mass and in the dorsal region of the body the hæmocœle is largely filled up by the peculiar form of connective tissue which I have previously described (2, p. 861) as metabolic tissue. In the Helicinidæ the tissue is of precisely the same nature as in Neritidæ, and it is not necessary to describe it again. It evidently consists in large part of reserve tissue, for it is most abundant in immature specimens in which the gonads and gonaducts are but slightly developed, and is much less abundant in sexually mature specimens. This metabolic tissue is specially concentrated round the larger blood-vessels.

It is not possible to trace the course of the blood-vessels by dissection of spirit-preserved specimens and only the larger vessels can be traced in sections. The following account of the circulation embodies as much information as I have been able to

obtain by reconstruction of sections. The ventricle is continued forward into a short and wide aorta, which immediately after passing through the pericardial wall—which it does at about the level of the hinder end of the left columellar muscle—divides into three principal branches. The one passes to the right towards the stomach, and, entering the visceral mass, divides into a number of branches which are distributed to the stomach, the intestine, the right lobe of the liver, the gonad, and the hypobranchial gland and gonaducts. The left branch runs forward for a short distance and then turns downward into the visceral mass and chiefly supplies the left lobe of the liver. A branch is directed towards the posterior part of the left columellar muscle. The third vessel is an almost direct forward continuation of the aorta and runs up in the dorsal region of the body towards the œsophagus; it passes above this organ and runs over the surface of the radular sac, to which organ it becomes firmly attached at about the level of the hind end of the pharyngeal bulb. Here it passes into a number of lacunar passages, supplying the pharyngeal bulb and the œsophageal pouches, and eventually makes communication with the large blood-space surrounding the nerve-centres of the head. This space in turn communicates freely with the lacunæ surrounding the pedal nerve-chords.

In this labyrinth of blood-channels I have not been able to recognize those by which the blood is collected and brought back from the various organs to the organ of respiration, the mantle. The principal hæmocœlic spaces or blood-sinuses are the following: (1) a pedal sinus, surrounding the pedal nerve-cords; (2) a subœsophageal sinus, underlying the buccal mass and œsophagus; this is continued back into (3) a circum-intestinal sinus, in which lie the coils of the intestine and the posterior part of the radular sac; (4) a peri-gastric sinus surrounding the stomach; (5) a recto-genital sinus, running the whole length of the rectum and gonaduct. The last named is evidently the pulmonary vein of Isenkrahe ("längs des Darmes zieht sich die Lungenvene hin"), but it does not carry back blood from the mantle to the auricle. On the contrary, it is easy to see that blood passes from it to the numerous fine blood-vessels or rather blood-spaces, for they have no definite walls, in the roof of the pulmonary chamber. The efferent pallial vein that collects blood from the mantle and returns it to the heart is on the opposite or left side of the mantle-cavity. It is a direct continuation of the auricle and can easily be traced forward in the left corner of the mantle-cavity, running along the upper border of the left columellar muscle (Pl. XXXII. fig. 16, *v. pal.*) nearly as far as the thick muscular anterior border of the mantle. It receives numerous vessels from the mantle, especially in the anterior part of its course. The blood from the intestinal and perigastric sinuses does not pass straight to the mantle, but is collected into a large sinus provided with definite walls (Pls. XXXIII. & XXXIV.

figs. 19 & 21, *v. ren.*), whence it passes by an afferent renal vessel to the glandular portion of the kidney. So far as I can ascertain, the blood is returned from the kidney to numerous small vessels running in the floor of the posterior half of the mantle-cavity, and is conveyed from these to the auricle by a distinct vein (Pl. XXXIII. fig. 20, *v. post.*) which opens into the hinder part of the auricle, and receives in addition blood from the roof of the extreme hind end of the roof of the mantle-cavity. There are thus two distinct vessels opening into the auricle, the foremost of which brings back blood from the roof of the greater part of the pulmonary chamber; the hindmost brings blood that has passed through the kidneys, then through the vessels on the floor of the pulmonary chamber, and in addition a small quantity of blood from the roof of the extreme hind end of the pulmonary chamber.

The Excretory Organs.

The topographical relations of the kidney, as compared with that of the Neritidae, have already been explained (p. 765). Regarded in detail, the kidney consists of a thick-walled glandular portion and a thin-walled non-glandular portion which serves as a bladder and urinary duct. The glandular portion is a large and, roughly speaking, quadrangular sac lying in the lower part of the visceral mass, below the stomach but above and somewhat to the left of the lower loop of the rectum. Its posterior and left wall fits closely against the pericardium and forms the inner boundary of the latter. The two ends of the sac are produced into large pockets or recesses, which partly extend round and embrace the walls of the pericardium (Pl. XXXIII. figs. 18 & 19), and partly extend upwards round the sides of the pyloric division of the stomach (Pls. XXXIII. & XXXIV. figs. 17 & 24). The cavity of the sac is spacious, and only partially subdivided by folds projecting inwards from the wall on the pericardial side; the opposite wall is not folded. The renal blood-vessels run in these folds.

The whole cavity, including the folds, is lined by a uniform glandular epithelium consisting of large irregularly shaped cells, of varying length, their free ends rounded or club-shaped and often projecting far into the lumen of the sac.

The characters of these cells are shown for *Alcudia* in fig. 22 and for *Lucidella* in fig. 23 (Pl. XXXIV.). In all the other species that I have examined the kidney-epithelium resembles that of *Lucidella*; it is only in *Alcudia* that the cells are as long, irregular, and amoeboid-looking as those drawn in fig. 22. In both cases the cytoplasm is clear and distinctly and coarsely vacuolated; the nucleus spherical, vesicular, with a few granules of chromatin. The ureter or non-glandular part of the kidney arises from the upper corner of the left-hand recess of the glandular sac. Its walls are composed throughout of a non-ciliated, very low, cubical epithelium, the cells of which are so much flattened that they might almost be called a pavement-

epithelium. The ureter is a widish tube which after leaving the glandular sac turns back to run round the hinder wall of the pericardium, interposing itself between it and the lower surface of the visceral mass. After passing from the left to the right side it mounts upwards again, passes under the reno-pericardial canal, and opens into the right-hand side of the mantle-cavity by a thick-lipped slit-like uropore. As is shown in fig. 23, the mantle-epithelium is invaginated at the lips of the uropore, and this invaginated portion is ciliated, but there is no uropore-sac such as I have described in the Neritidæ.

The reno-pericardial canal (figs. 19 & 22) opens out of the lower part of the right-hand recess of the glandular part of the kidney, and runs straight into the right side of the pericardium opposite the middle of the expanded base of the auricle. The canal is short, straight, and narrow, lined by a cubical ciliated epithelium, the component cells of which are small and bear no resemblance to the very large ciliated cells lining the long twisted reno-pericardial canal of the Neritidæ. The cilia are fine and directed towards the kidney. A thickening of the epithelium at the pericardial opening of the canal is suggestive of the presence of a pericardial funnel. The structure and relations of the kidney and the reno-pericardial duct are remarkably uniform in all the species of Helicinidæ that I have examined.

The Generative Organs.

Thiele (10) has shown that the female ducts are monaulic in *Hydrocena cattaroensis*, but diaulic in *Helicina kubaryi*. Before my memoir on the Neritidæ was published I had discovered the diaulic ducts in *Alcudia* and *Eutrochatella*, but, as I omitted to make mention of them in that place, I must yield priority to Thiele, whose diagrammatic figure (*loc. cit.* text-fig. 2) gives a correct representation of the general relations of the various subdivisions of the ducts. But it is almost impossible to construct a life-like picture of such complicated organs from a study of sections, and as I have dissected out the gonaducts, both male and female, in a number of species and have checked my observations by the study of sections, I may be pardoned for again taking up the subject and entering into it at some length. From the analogy of the Neritidæ, in which family the gonaducts exhibit a considerable range of variation, I expected to discover equally great differences in these organs in the various genera of Helicinidæ, but have been disappointed. There are differences, it is true, but they are slight and do not throw much light upon the systematic affinities of the various genera studied.

The gonads in all Helicinidæ lie above and to the right side of the liver. The ovaries are follicular, and the follicles open into a large thin-walled chamber which in *Alcudia* and *Eutrochatella* is situated on the right side of the visceral mass, just behind the posterior end of the right columellar muscle and in front of the

muscular partition separating the visceral cavity from the complex glandular mass formed by the hypobranchial gland and gonads (Pl. XXXVI, fig. 32). The ova appear to go through their maturation-phases in this chamber, as no ripe ova are to be seen in the follicles. In *Alcadia* and *Eutrochatella* this ovarian chamber is sac-shaped and on the right side of the body, but in Pacific and Oriental species, such as *Palæohelicina ida*, *Orobophana ponsonbyi*, and *Aphanoconia gouldiana*, the ovarian chamber is produced into a wide tube which stretches transversely across the body and receives the products of the follicles of a left ovarian lobe, the latter being a distinct triangular lobe, projecting from the surface of the visceral mass and packed close under the left columellar muscle. This lobe is possibly characteristic of Pacific and Oriental species: it is absent in *Alcadia*, and scarcely represented in *Eutrochatella*. My specimens of *Lucidella* were all male, and therefore I cannot say whether it occurs or not in this West Indian genus. The female gonads of *Alcadia hollandi*, which are to all intents and purposes identical with those of *A. palliata*, are depicted in Pl. XXXV, fig. 25; and figs. 30 to 35 (Pls. XXXV. & XXXVI.) represent selected sections from a series passing horizontally through the genital complex of a female of the same species, fig. 30 being the uppermost and fig. 35 the lowest of the series.

Dealing first with the macroscopical characters, the following organs or parts can be distinguished, and as their shape and relative positions are clearly indicated in fig. 25 a detailed description will be superfluous. (1) The oviduct *od.* is a very narrow duct leading from the ovarian chamber to (2) the dilated or V-shaped portion of the oviduct, in which a descending limb (*od.*¹) and an ascending limb (*od.*²) can be recognized. In *Alcadia* the ascending limb is as long and of approximately the same diameter as the descending limb: in its lowest third it receives the short and narrow duct of a globular receptaculum seminis. (3) The ootype, *oot.*, is a long, more or less dilated glandular duct running parallel with the rectum in the right hand of the roof of the mantle-cavity, and opening into the latter on the right side by a relatively narrow aperture on a papilla which lies in a sort of shallow cloaca formed by the expanded lips of the rectal opening. Into the posterior end of the ootype open: the ascending limb of the V-shaped part of the oviduct; the cæcum of the ootype, a sac-shaped structure of considerable relative size, which lies parallel to and to the inner side of the V-shaped duct; thirdly, the short and rather narrow duct of (4) the vagina, *vag.* The last named is a slender duct with thin walls, opening into the mantle-cavity close to the aperture of the hypobranchial gland. It is continued posteriorly into a sac, which runs back on the outside of the V-shaped duct and ends blindly (this sac has been displaced in fig. 25 to show it more clearly, in its natural position it would be concealed by the V-shaped duct). It may be called the vaginal sac. Comparing these ducts with those of the Neritidæ, particularly with *Paranerita* (2, fig. 60), it is clear that the ootype is

homologous in the two forms, as is also the vagina. The vaginal sac of *Alcadia* corresponds to the spermatophore sac of *Paranerita*, but in the former genus the duct connecting the vagina with the ootype has been shortened to such an extent that it is merely a passage between the two. The V-shaped duct of *Alcadia* is only a modification of the oviduct and has no exact homologue in *Paranerita*; the position of the receptaculum seminis is also somewhat different. There is no trace of an oviduco-cœlomic funnel in any Helicinid, nor is there any representative of the crystal-sac. On the other hand, the cœcum of the ootype is not represented in the Neritidæ, for it would be straining homology too far to suggest that it is the equivalent of the lower dilated part of the ductus enigmaticus. But if the morphological comparison between the female gonaducts of the Neritidæ and Helicinidæ is fairly obvious, a physiological comparison is by no means so clear. In the specimen of *A. hollandi* whose ducts are drawn in fig. 25 the hinder moiety of the ootype was filled and greatly distended by a large mass of spermatozoa held together by a coagulable substance, and, as shown in the figure, a string of the same mass of spermatozoa and coagulum extended into and filled the cœcum of the ootype. The vaginal sac was empty, but the receptaculum was full of spermatozoa. This suggests that the "ootype" is the copulatory canal or functional vagina, and that the "vagina" may serve for the passage of the ova into the mantle-cavity. But the probability of such a conclusion is lessened by the fact that in *Aphanoconia merguiensis* and *A. gouldiana* I found the vagina and vaginal sac full of spermatozoa. I have not found ova either in the oviduct or in the ootype of any of my specimens; and apparently in the Helicinidæ fertilization is not effected by means of spermatophores, for I have found no trace of such structures. The mass of spermatozoa and coagulum in *Alcadia hollandi* cannot be called a spermatophore. The evidence as to the function of the several parts being slender, and what there is conflicting, I offer no definite theory on the matter, but may add that the "vagina" is evidently a distensible duct, as it has thin walls, with a very feeble coat of circular muscle-fibres, but with a number of muscular slips passing from its walls to be attached to adjacent organs. On the other hand, the ootype has a thick muscular coat, especially in its hinder moiety, and the contraction of this muscular coat would expel any contained material through the external aperture.

A comparison of the gonaducts of the several genera shows certain differences in detail. The female gonaducts of *Eutrochatella*, a West Indian genus, are shown in Pl. XXXV. fig. 26. Their arrangement is clearly very similar to that of *Alcadia*. The ascending limb of the V-shaped duct is shorter in *Eutrochatella* and has more the appearance of a direct posterior continuation of the ootype. The receptaculum seminis is small and ovoid, but in the same position as in *Alcadia*. The vagina is short; the vaginal sac of moderate length. The cœcum of the ootype is a large

flattened sac and extends some way behind the posterior end of the V-shaped duct.

Of the Pacific and Oriental genera, *Aphanoconia* (Pl. XXXV. fig. 27) most nearly resembles *Alcadia* and *Eutrochatella*. The descending limb of the V-shaped duct is large; the ascending limb short and scarcely differentiated from the hinder end of the ootype; it bears a relatively large globular receptaculum seminis. The vagina is fairly long, and opens by a very short transverse duct rather high up into the ootype. The vaginal sac is short. There is no cæcum to the ootype. The female ducts are very similar in all the four species of *Aphanoconia* that I have examined, differing chiefly in the relative length of the vaginal sac and the position of the vagino-ootypal connection.

On the other hand, *Palæohelicina* (fig. 28) and *Orobophana* (fig. 29), while resembling one another, differ in some important respects from the West Indian genera and from *Aphanoconia*. In *Palæohelicina idæ* the ascending limb of the V-shaped duct is wide and scarcely differentiated from the hinder end of the ootype. There is no receptaculum seminis, but the ootypal cæcum is large, bilobed at its extremity, lined by an epithelium of peculiar character, and filled with spermatozoa. It evidently functions as a receptaculum seminis. The vagina and vaginal sac are normal. In *Orobophana ponsonbyi* the descending limb of the V-shaped tube is unusually long; the ascending limb very narrow and short, and does not bear a receptaculum seminis. The cæcum of the ootype is large, bilobed, full of spermatozoa, and in every respect similar to that of *Palæohelicina*. The vagina is long; the vaginal sac leaves it about halfway between its external aperture and its connection with the ootype.

I am unable to give a description of the female organs of *Lucidella aureola*, as all my specimens were males.

Summing up the above facts, we see that as regards the structure of the gonaducts there are two types in the genera dealt with. In the first type there is a receptaculum seminis on the ascending limb of the V-shaped duct. This type is divisible into two sub-types: the one, found in *Alcadia* and *Eutrochatella*, is characterized by the large caecal appendage of the ootype; the other, found in *Aphanoconia*, has no such cæcum. In the second type, represented in *Palæohelicina* and *Orobophana*, there is no receptaculum seminis on the ascending limb of the V-shaped duct, but this organ is replaced functionally by the modified bilobed cæcum of the ootype. According to Wagner (12) *Palæohelicina* stands nearest to *Helicina sensu restricto*, and therefore nearer to *Alcadia* than other Oriental and Pacific forms, but in the structure of the female gonaducts, *Aphanoconia* stands nearest to *Alcadia*, but *Palæohelicina* with *Orobophana* stand somewhat apart.

The gonaducts of the Helicinidæ evidently undergo great histological changes at the onset of sexual maturity. In sections of immature females of *Alcadia* and *Eutrochatella* the ootype is a

relatively narrow tube lined by a columnar epithelium, in which glandular elements are hardly recognizable, and there is a similar lack of differentiation of glandular cells in the V-shaped duct. On the approach of sexual maturity the epithelium of the ootype is enormously thickened, is rich in glandular elements, and is thrown into complicated folds; at the same time, histological changes occur in the V-shaped duct. In the breeding-season, when the ootype is distended as shown in fig. 25 (Pl. XXXV.), the epithelial folds of the ootype disappear, the gland-cells have discharged their contents, and the epithelium appears shrunken and thinner than before. In consequence of these changes, it is difficult to give a consistent account of the histological characters of the ducts: what follows is based on a series of sections of a mature specimen of *Alcadia hollandi*, in which the tissues, thanks to Mrs. Longstaff's care, are admirably preserved.

In the distal half of the ootype, that is in the portion marked *a* in fig. 25, the epithelium is moderately long and of the mixed glandular and ciliated kind. The ciliated cells are elongate columnar, not much attenuated at their bases, their cytoplasm clear and very finely granular, their nuclei rather large, oval, situated rather to the basal side of the middle of the length of the cell. The gland-cells are of nearly the same shape, but of rather greater diameter than the ciliated cells, their nuclei slightly larger, situated nearer the bases of the cells, and the cell-body filled with rather small highly refracting spherules of a greenish-yellow colour in preparations stained with hæmatoxylin and eosin. The hinder moiety of the ootype—namely, that portion filled with the mass of spermatozoa in fig. 25—shows somewhat different characters. The supporting epithelial cells are, as before, columnar and finely granular, but of greater length: they appear to have lost their cilia over the greater part of the inner wall of the ootype and to end distally in rounded and somewhat vacuolated extremities, but as I can find cilia in patches this appearance may be due to maceration. The gland-cells in this region (Pl. XXXVII. fig. 36) are not very abundant, but characteristic, and presumably mucinogenous as they stain deeply in hæmatoxylin. Their basal ends, resting on the basal membrane, are broad and in each is a rather small subspherical nucleus, above which the cell tapers to a fine tube filled with a darkly staining granular material: these attenuated cell-bodies run between the supporting cells and terminate in swollen extremities filled with coarse deeply staining spherules. Throughout this region of the ootype the epithelium is thrown into ridges and furrows, which are partly due to the folding of the walls, but chiefly to the unequal length of the epithelial cells. At the hinder end the folds increase and there is a prominent valve projecting into the lumen and making a complete spiral turn just above the opening of the V-shaped duct. This opening, guarded by the above-mentioned valve, is narrow. The upper part of the V-shaped duct is lined by an epithelium of the same character as that of the hinder moiety of the ootype, the

supporting cells being here distinctly ciliated and the deeply staining mucinogenous cells conspicuous. This epithelium is thrown into a distinct spiral ridge, which winds round the upper part of the V-shaped duct nearly as far as the entrance of the duct of the receptaculum seminis. Here the epithelium changes its character; the deeply staining mucinogenous cells disappear and give place to very numerous long tubular gland-cells with large oval basal nuclei, the tube-shaped cell-body coarsely alveolar and the alveoli containing large refringent non-staining spherules. Wedged between these are the ciliated cells, with elongated nuclei at about the middle of their length, very attenuated basal ends, and somewhat expanded wedge-shaped distal ends, each with a distinct striated border and a tuft of fairly long cilia. The receptaculum seminis (Pl. XXXVII. fig. 37) is lined by a low columnar ciliated epithelium of uniform character. The cell-bodies are finely granular and stain readily; the nuclei spherical and deeply staining. Each cell has a distinct striated border and bears a tuft of long coarse cilia. The spermatozoa in the receptaculum are all arranged with their heads directed towards the centre, their tails outwards and entangled among the cilia of the epithelium. The receptaculum and its duct are invested by a very stout coat of muscular fibres.

The transition from the upper end of the ascending limb of the V-shaped duct to the narrow tube of the oviduct is abrupt. The oviduct is lined throughout by an epithelium consisting of long columnar cells bearing specially long and coarse cilia. The characters of these cells are shown in fig. 38 (Pl. XXXVII.).

The cæcum of the ootype is lined by an epithelium differing from that of the rest of the ootype in the absence of glandular cells. The walls of the cæcum, like those of the hinder moiety of the ootype itself, are provided with a tolerably thick coat of muscular fibres, mostly disposed circularly. The muscular coat is not folded, but the epithelium is disposed in longitudinal ridges due, as seen in fig. 39 (Pl. XXXVII.), to the greater length of the cells composing them: this figure is from *Orobophana ponsonbyi* and not from *Alcadia*; in the latter genus the cells are somewhat longer and more slender, but otherwise similar in character. As is shown in the figure, the cells are club-shaped with rounded ends projecting into the lumen of the cæcum; they do not bear cilia. It is the presence of this characteristic epithelium in the bilobed sac full of spermatozoa leading into the hinder end of the ootype in *Palæohelicina* and *Orobophana* which leads me to identify the sac in question with the cæcum of the ootype of *Alcadia* and *Eutrochatella* rather than with the receptaculum seminis, and it is further to be remarked that in the non-ciliated bilobed sac the spermatozoa are arranged pell-mell, with their heads and tails in all directions instead of being definitely oriented as they are in the ciliated receptaculum seminis.

The distal third of the vagina is lined by an epithelium consisting for the most part of highly vacuolated clear cells with basal nuclei,

and between these are very attenuated supporting cells. I could not detect any cilia on the latter.

The proximal two-thirds of the vagina and the vaginal sac are lined by a non-ciliated epithelium of uniform character, the details of which were not well preserved in my sections of *Alcadia* and *Eutrochatella*: apparently they had been injuriously affected by the action of Perenyi's fluid. In *Orobophana ponsonbyi* the epithelial cells of the lower part of the vagina and of the vaginal sac are squarish in outline, non-ciliated and clearly glandular, for each contains a number of coarse non-staining spherules. The cavity of the sac contains a number of spherules of similar character and among them ropy masses of some coagulable substance staining faintly in hæmatoxylin.

In *Orobophana* the epithelial lining of the ootype differs in some respects from that described for *Alcadia*. The supporting cells are attenuated towards their bases, have long compressed nuclei about the middle of their length, and are distinctly ciliated. The gland-cells of the distal part of the ootype resemble those of *Alcadia*, but are apparently differentiated to some extent, for the granular contents of those on the inner side of the ootype nearest the mantle-cavity are eosinophilous, those on the outer side are not. Just above the entrance of the vaginal duct the eosinophilous cells are replaced by mucinogenous cells staining deeply in hæmatoxylin. A large spiral flap or valve separates the opening of the cæcum from that of the ascending limb of the V-shaped duct. The last named is very narrow and invaginated for some distance into the terminal part of the ootype: it has no spiral epithelial fold, such as is seen in *Alcadia*. The gland-cells of the distal limb of the V-shaped tube are highly eosinophilous.

Thiele (10) has shown that the female ducts of *Hydrocena* are monaulic. The external aperture leads into a thick-walled glandular duct, which is clearly homologous with the ootype of the Helicinidæ. The lumen of this duct is continued posteriorly into a fairly wide canal lined by a columnar epithelium devoid of glandular cells, and this ends in a saccular dilatation of considerable size, which is apparently glandular; "sein Epithel enthält Klümpehen von Körnchen." Thiele identifies this sac and its duct with the vaginal sac and vagina of *Helicina*, and regards it as the homologue of the right kidney of the Trochidæ, which in this case has not acquired an independent opening into the mantle-cavity. In addition to this sac, three other structures open into the hinder end of the "ootype" in *Hydrocena*: on the right a thick-walled glandular cæcum; on the left the oviduct; and between the two and dorsad of the "right kidney sac" a tubular receptaculum seminis. Thiele's homologies seem to be perfectly just, and after his discovery of the conditions obtaining in *Hydrocena*, I must agree with him in regarding the vaginal sac of the Helicinidæ and the spermatophore sac of the Neritidæ as the representatives of the right kidney. But I still beg leave to differ from his interpretation of the vaginal aperture as the

primitive aperture of the right kidney, and of the external aperture of the ootype as a secondarily acquired separate genital duct. The conditions in *Hydrocena* appear to me to be an ample justification of the argument put forward in p. 873 of my memoir on the Neritidæ. *Hydrocena* is in many respects more primitive and therefore more nearly related to the ancestral Neritoid stock than the Helicinidæ, and Thiele himself points to the generative organs as one of the evidences of primitive organization.

In his memoir entitled "Die systematische Stellung der Solenogastren und die Phylogenie der Mollusken" (9) Thiele, after describing the male organs of *Septaria*, gives the following account of the male organs of *Helicina* (= *Waldemaria* Wagner) *japonica*: "Bei *Helicina* ist der männliche Geschlechtsapparat merklich einfacher, der Samengang ist nur sehr wenig aufgeknäuelnd und weiter, er mündet in den Drüsengang von unten und rechts nicht weit vor seinen Hinterende. Der letztere ist bedeutend einfacher als bei *Varicella*, durch Falten streckenweise etwas zertheilt, doch scheint das drüsige Epithel trotz geringer Verschiedenheiten an manchen Stellen im Wesentlichen gleichartig zu sein. Die Drüsenzellen liegen durchweg zwischen den Stutzellen. Dieser Gang reicht weit nach vorn in der Mantelhöhle doch habe ich ein besonderes Kopulationsorgane nicht wahrgenommen. Die ektodermale Drüse, welche rechts von Hinterende des Drüsenganges (Prostata) in die Mantelhöhle ausmündet, erstreckt sich, in dem sich allmählich grosser wird, weit nach hinten, wo sie neben dem Hinterende der Niere aufhört. Nach ihrem Bau ist an ihrer ektodermalen Herkunft nicht zu zweifeln, da sie zwischen den grobkörnigen Drüsenzellen deutliche Stutzellen enthält. Sie mag als eine Art von Manteldrüse ähnlich der Hypobranchialdrüse anzusehen sein: ihre Funktion ist unbekannt."

The ectodermal gland referred to in this passage I have already described as the hypobranchial gland, fully agreeing with Thiele's interpretation of it. It has no connection with the generative organs. In the six genera that I have examined the male ducts are, with the exceptions to be mentioned hereafter, very much alike, but not quite so simple as Thiele's description would lead one to suppose, and presumably *Waldemaria japonica* has undergone some simplification in these organs, for so accurate an observer cannot have overlooked the accessory organs that I am going to describe.

The testis, like the ovary, is follicular in structure; fine thin-walled ducts converge from the follicles and unite in the right side of the visceral mass to form the sperm-duct. The last-named organ occupies a position similar to that of the oviduct in the female: in immature specimens it is slender, slightly convoluted, and lined by a columnar ciliated epithelium. In mature specimens its middle portion is greatly distended by spermatozoa, is considerably convoluted, and the ciliated epithelial lining is no longer distinguishable. The sperm-duct tapers somewhat and, as Thiele describes, opens into the lower and right side of a long glandular

thick-walled sac, some little distance in front of the hinder end of the latter. This thick-walled sac, which is evidently the representative of the ootype of the female and of what I have called the terminal chamber in the Neritidæ, runs forward in the roof of the mantle-cavity, below and to the right side of the rectum, and opens into the mantle-cavity by a terminal pore situated close to the anus. At about one-third of its whole length from the external aperture, the thick-walled sac—which I shall call the terminal sac of the sperm-duct or, more shortly, the terminal sac—is joined by another sac of considerable diameter. This second sac, which I shall call the diverticulum, opens into the terminal sac by a wide aperture, and runs back close to the right side of the latter, to end blindly, sometimes just in front of the entry of the sperm-duct into the terminal sac (*Aphanoconia gouldiana*, Pl. XXXVII. fig. 41); in other cases, however, it extends as far back as the hinder end of the terminal sac, and may even project a little beyond it (*Alcadia hollandi*, fig. 40). The anterior third of the terminal sac, in front of the entry of the diverticulum, exhibits three or four deep transverse constrictions: in section it is round or oval, and the lumen is partly occluded by deep longitudinal folds projecting into it. These folds are covered by a mixed glandular and ciliated epithelium: the ciliated cells of the familiar kind with attenuated basal ends, the gland-cells tubular with basal nuclei and vacuolated cell-bodies, in which no secretory granules could be distinguished in well-preserved specimens of *Eutrochatella*. In its posterior two-thirds the terminal sac is laterally compressed so as to be elongate oval in section, and it gives off from each end of the oval and from the adrectal side numerous short hollow caecal outgrowths which are sometimes branched, especially in *Aphanoconia* (fig. 41). Internally the longitudinal epithelial ridges die out in the posterior two-thirds of the terminal sac, but the epithelial lining both of the cavity of the sac and of the caecal outgrowths is of very nearly the same character as that of the anterior third. The supporting cells are distinctly ciliated. The epithelium of the diverticulum differs from that of the terminal sac only in the fact that the gland-cells are full of eosinophilous granules, and the cilia of the supporting cells are longer and rather coarser. The above characters hold good for all the species that I have examined, the differences between them being too slight to deserve mention. It may be noted that in *Alcadia* the hinder moiety of the diverticulum is constricted at very regular intervals (Pl. XXXVII. fig. 40). Both in *Eutrochatella* and *Lucidella* I have found in sections a second diverticulum in the form of a slender thin-walled tube opening into a recess of the terminal sac at the same level as, but on the opposite side to, the diverticulum above described. The walls of the recess are lined by a glandular epithelium staining deeply in eosin. The narrow tube runs back in the mantle-wall nearly parallel to the terminal sac and ends blindly just in front of the aperture of the hypobranchial gland. Its hinder end touches and appears to be adherent to the sub-epithelial muscular

wall of the mantle-cavity, but there is no aperture into the mantle. I have not been able to find this tube in other species, but this may be due to the imperfection of my sections and to the fact that it is too small to be recognizable in dissections. It is a well-defined structure in *Eutrochatella* and is lined throughout by a non-glandular cubical epithelium. I am inclined to the opinion that the anterior third of the terminal sac of the male is the equivalent of the body of the ootype of the female; the diverticulum of the male represents the cæcum of the ootype, and the narrow tube (Pl. XXXVII. fig. 42, *k.r.*) represents the vagina of the female, but has lost its opening into the mantle-cavity. If this identification is correct, a relic of the right kidney-sac is retained in the male, at least in *Eutrochatella pulchella* and *Lucidella aureola*.

It may be noted that Isenkrahe's drawing of the male organs of *Helicina titanica* is very nearly correct.

The Nervous System.

Nobody has given a detailed account of the nervous system of any Helicinid since Bouvier dealt with this subject in his classical memoir on the nervous system of Prosobranch Gastropods (3). In that work he gives an elaborate figure of the nerve-centres and principal nerve-trunks of *Helicina sagraiana* d'Orb., and also several figures of the buccal ganglia of the same species and of the cerebral and pleuro-pedal centres of *H. brasiliensis* Gray. As is always the case, Bouvier's figures possess a high degree of accuracy, and if I have some criticisms to offer, they must not be taken as depreciatory of his excellent work, but as an elaboration of it, rendered possible by careful study of sections and by the opportunities for exceedingly fine dissection afforded by the Braus-Drüner microscope.

In the first place, it was necessary to determine whether the supra-intestinal nerve exists in the Helicinidæ. Bouvier had failed to find it in the Neritidæ, and when in a subsequent memoir he announced its discovery in the latter group, he hazarded the opinion that it would probably be found in the Helicinidæ. But it does not exist in these pulmonate rhipidoglossates; it has disappeared in them as completely as the organs with which, when present, it is associated, the ctenidium and the osphradium. I can speak with certainty on this point, for I have made so many dissections and have studied such a sufficient number of serial sections that I could not have overlooked it if it were present.

In the second place, I am unable to verify some of the details of Bouvier's figure of the nervous system of *H. sagraiana*. In none of the species that I have studied are the pedal, pleural, and subintestinal centres as distinct as shown by him. As may be seen in fig. 44 (Pl. XXXIX.), the pleural ganglia are ill-defined swellings, scarcely distinguishable from the swollen anterior ends of the pedal cords, and the subintestinal ganglion is so intimately fused

with the pleurals that it is unrecognizable as a separate ganglion, even in sections (Pl. XXXVIII. figs. 45 to 52). The pedal cords, though not so widely separated in any of the species of Helicinidæ that I have dissected as in the Neritidæ, are not so closely approximated as shown in Bouvier's figure. They are fairly close together and nearly parallel to one another in *Eutrochatella pulchella*, somewhat more divergent in *Alcadia hollandi*, further apart in *A. palliata*, and widely divergent in *Aphanoconia andamanica*. The actual amount of divergence or approximation is, however, undoubtedly dependent on the degree of contraction of the muscular mass of the foot, and is a character of no great importance. If the foot is much contracted the pedal cords are approximated and the numerous and slender pedal commissures are arched; if the foot is relaxed the cords are further apart and the commissures are pulled out straight. I cannot but think that Bouvier has exaggerated the length of the cerebro-pleural and cerebro-pedal connectives. In none of the species that I have examined are they appreciably longer than the antero-posterior diameter of the cerebral ganglia, and in some species, e. g. *Lucidella aureola*, they are very short, but it is, of course, possible that they are unusually long in *H. sagraiiana*. In respect of the nerves issuing from the ganglionic mass formed by the fusion of the anterior ends of the pedal with the pleural centres, Bouvier, while otherwise exact, makes one important omission. He does not figure or describe a relatively large pair of nerves which originate one on each side of the most anterior pedal commissure from the dorsal surface of the swollen anterior ends of the pedal cords. Each of these nerves (Pl. XXXIX. figs. 43 & 44, *n.op.*) passes outwards and backwards, penetrates the muscular wall of the body, and passes to the muscles of the operculum, hence the nerves in question may be called the opercular nerves. That of the right side breaks up into a number of fine twigs in the opercular muscles, that of the left side gives off a stout branch which passes to a peculiar hollow organ connected with a plate of cartilage near the left corner of the opercular lobe. This organ will be described in detail further on.

The otocysts are situated just above the origins of the two opercular nerves, and are therefore on the *dorsal* side of the pedal ganglia, as is shown in fig. 44. Bouvier, describing the otocysts of *Helicina brasiliensis* says "elles sont situées sous les cordons pedieux": and it is true that in a retracted specimen, in which the head has been drawn back behind the foot, so that the pedal cords appear to lie in front of the cerebral ganglia, one does find the otocysts below the pedal cords, when making a dissection from the dorsal side. But in such a case the sole of the foot is uppermost, and the morphologically dorsal side of the pedal cords is turned downwards, this change of position being very puzzling to the observer both in sections and dissections. It is worth remarking in this connection that in my experience the small Polynesian genera, *Aphanoconia*, *Palæohelicina*, and, in

a lesser degree, *Orobophana*, when they withdraw themselves into their shells, do not contract themselves as much as the West-Indian species. The sole of the foot in these Polynesian genera is longer and narrower than in the West-Indian genera, the columellar muscles longer and inserted further back from the mouth of the shell. There is therefore more ample room for the head and foot in the last whorl of the shell, and when the animal retracts itself the foot is scarcely at all contracted, but simply slides back with its sole applied to the outer side of the shell till the operculum borne on the broad opercular lobe closes the aperture. Specimens of these genera, when extracted from their shells, do not present the deformed appearance of an *Alcadia* or an *Eutrochatella*, the pedal nerve-cords are not turned forward with their morphological surfaces reversed, and if the animals were only a little larger they would be much easier to dissect than their American congeners. It is possible, and even probable, that these different modes of retreating into the shell, which are themselves dependent on the varying length and points of insertion of the columellar muscles, are correlated with the different forms of operculum upon which Wagner has founded his system. At any rate, they are consistent with it, but I have not been able to follow out this problem in detail.

To return to the nervous system. The opercular nerves must not be mistaken for the parietal nerves correctly described and figured by Bouvier and labelled *d'*, *e'*. The parietal nerves (Pl. XXXIX, fig. 44, *n.par.*) are much more slender than the opercular nerves and originate, as shown in fig. 44, from the pleural centres, between the great pallio-columellar nerves and the cerebro-pleural connectives. They pass to the muscular walls of the head behind the tentacles. From the ventral side of the swollen anterior ends of the pedal cords, in the same cross-section as the opercular nerves, a rather stout pair of nerves originates near the middle line; these nerves, which are shown in section in fig. 46 (Pl. XXXVIII.), pass to the pedal gland and appear to be specially connected with that organ.

As regards the subintestinal nerve and its distribution, I am unable to bring my observations into agreement with those of Bouvier. The short nerve connecting the subintestinal with the left pallio-columellar nerve-trunk does not appear to be a constant feature. I have found such a connective in a single specimen of *Alcadia palliata*, and in that one instance it is much closer to the pleuro-pedal centres than is shown by Bouvier. But I can find no trace of it in any other specimen that I have examined. I am unable to find any trace of the visceral nerve labelled *j'* in Bouvier's figure, which he describes as given off from the left side of the subintestinal at some distance from the origin of the latter, and in general my observations on the subintestinal and visceral nerves differ so much from his that a detailed account is necessary. The figure illustrating this account (Pl. XXXIX, fig. 43) is founded upon dissections, and the ultimate ramifications of the principal

nerve-branches have been traced in sections. The subintestinal trunk in *Alcudia palliata*, *A. hollandi*, and *Eutrochatella pulchella*, after leaving the subintestinal ganglion, which latter is unrecognizably fused into the pleural centres, courses along the floor of the anterior division of the general body-cavity, below the pharyngeal bulb, the radular sac, and œsophagus. It keeps closer to the right than to the left columellar muscle, and on reaching the posterior end of the muscle it doubles the angle between it and the visceral mass, and entering the latter turns to the left and enlarges to form a ganglion of some size from which several nerves are given off. That this is a true ganglion-centre, and not a mere nodal thickening at a point from which several nerve-branches originate, is demonstrated by the considerable sheath of nerve-ganglion cells. The principal nerves issuing from the ganglion, in addition to the main trunk, are the following:—a small nerve, v^1 , which passes to the right near the surface of the visceral mass and is distributed to the gonads and liver. Another small nerve, v^2 , which passes to the left of the visceral mass and appears to innervate the right lobe of the liver and surface of the stomach. A stout nerve, *n. gen.*, which runs to the right, passes above the oviduct or sperm-duct, gives off a large branch to the mucous gland, and turns forward to break up into twigs on the posterior part of the complex of genital ducts: this is the genital nerve, and it identifies the ganglion from which it originates as the visceral ganglion. There is no separate genital ganglion as in the Neritidæ. The hinder end of the visceral ganglion is continued into a rather stout nerve, which may be regarded as the continuation of the main trunk of the subintestinal: this passes through the liver and below the small and large intestine, and turning towards the left it passes towards the lower border of the right moiety of the kidney, near which it enlarges to form a small but distinct ganglion, which I take to be the representative of the elongated visceral ganglion of the Neritidæ. From this ganglion small nerves are given off to the liver and kidney, and a larger nerve passes below the kidney, skirts the uropore, and can be traced beyond as far as the auricle of the heart, at which point it ceases to be recognizable. It is a matter of extreme difficulty to follow the above-mentioned nerves through the liver and intestinal coils by simple dissection, and I have only been able to make sure of their ultimate course by the study of serial sections.

After this criticism of the general characters of the nervous system, I may return to the consideration of some special details. The pleuro-pedal centres and with them the subintestinal ganglion are, as I have already said, so intimately fused as to be practically indistinguishable as separate ganglia. This fusion is brought out in a striking manner in sections. Figs. 45 to 52 (Pl. XXXVIII.) represent selected members of a series of nearly transverse sections through the pleuro-pedal centres of *Alcudia hollandi*. Fig. 45 represents a section through the pedal cords at the point where they begin to diverge from one another. Dorsad

of them are the otocysts, *ot.*; ventrad of them is the pedal gland. Each cord consists of a core of nerve-fibres and dendrites surrounded by a cortical layer of nerve-ganglion cells. The latter send in lateral horns at about the middle of the outer side of each cord in such a manner as to divide the central core into upper and lower moieties, which have been identified by French authors with the pleural and pedal sections of the cords respectively. This interpretation, however, does not appear to me to be well founded. Fig. 46 represents a section somewhat further forward than that in fig. 45; it passes through the hinder part of the anterior pedal commissure, and includes the roots of the two nerves of the pedal gland and of the right opercular nerve. The nerve-fibres of the former are seen to be supplied from two areas of the cortical layer lying respectively on the outer and inner sides of the ventral side of the cord. The opercular nerve receives its fibres partly from a centre on its own side, partly from a centre on the opposite side of the cord, the latter fibres crossing over in the commissure. Below them is a stout band of commissural fibres connecting the lateral horns of nerve-ganglion cells with one another. Above the median ventral raphe is a thick mass of nerve-ganglion cells. In a section somewhat further forward (fig. 47) the ventral raphe has disappeared and the mass of ganglion-cells above it is only represented by two small islets of nerve-ganglion cells, which are separated from the ventral surface by two well-defined bands of nerve-fibres starting from the ventro-lateral groups of nerve-ganglion cells and passing towards the centre partly decussate, partly sweep round the islets to curve round to the lateral horns of the ganglion-cells. Above these curved bands is the well-defined transverse commissural band of nerve-fibres, and above this again there is on either side a centre, consisting of nerve-fibres overlaid by a layer of ganglion-cells, which is seen to be connected with the origins of the opercular nerves. Above the nervous mass a pair of muscular cords passing from the otocysts towards the centre should be noticed.

In the next section (fig. 48), taken some little way further forward, the two little islets of ganglion-cells lying opposite the lateral horns are still visible. Below them are transverse bands of commissural fibres. Between them is seen the most anterior part of the decussating tract observed in the previous section. After decussation the fibres sweep out right and left to the dorso-lateral regions. In the mid-dorsal line is a deep and wide groove into which the muscular cords noted in the last section are entering. I regard the whole of the sections hitherto described as belonging to the pedal centres. The next section (fig. 49) shows that the dorsal groove containing the two muscular cords has been converted into a canal by the upgrowth and dorsal union of the nervous tissue. All that lies below this canal belongs to the pedal centres; all that lies to the sides of and above the canal belongs to the pleural centres.

In the pedal centres a prominent bundle of nerve-fibres is being formed on either side of the middle line: these when traced forward prove to be the origins of the cerebro-pedal connectives. Above them are the remains of the transverse anterior pedal commissure. Laterally, above the lateral horns of the ganglion-cells two other tracts of nerve-fibres are making their appearance: these have evidently received large contributions from the decussating fibres noticed in the previous sections, and when traced forward they prove to form part of the cerebro-pleural connectives. The central canal containing the two muscular cords is surrounded by a layer of nerve-ganglion cells, thickest on the ventral side, and above the canal are seen tracts of nerve-fibres originating from the lateral horns of either side and passing towards the middle line. Above them, again, is a small transverse band of commissural fibres, and above these a fairly thick layer of ganglion-cells, which, as may readily be seen by comparing this with the preceding sections, is something added to what was there before, and is, in fact, the layer of pleural ganglion-cells. The next three figures (50, 51, and 52) explain themselves. In fig. 50 the pedal centres are diminishing rapidly in volume. On the left side, which, owing to the sections being somewhat oblique, is rather behind the right side, a large tract of vertical nerve-fibres is seen passing from the pedal to the pleural centres. To the outside of this above the lateral horn are tracts of fibres some of which run upwards and will pass into the left pallio-columellar nerve, others will be continued into the right cerebro-pleural connective and the right parietal nerve. On the right side the origins of the cerebro-pedal and cerebro-pleural connectives are well defined. Between them lie the ganglion-cells of the lateral horn, and above the nucleus of the cerebro-pleural connective is a second lateral ingrowth of nerve-cells, belonging to the pleural ganglion. The pleural centre of nerve-fibres is well marked, and from it a stout band of commissural fibres passes above the central canal to the pleural centre of the other side. This is the pleural commissure, which I have already described in *Neritidæ*. Fig. 51 shows the cerebro-pedal and cerebro-pleural connectives in cross-section. The central canal with its contained muscular slips, having passed through the ring formed by the pleural and pedal centres, emerges as a groove on the ventral side. The origins of the right parietal and right and left pallio-columellar nerves are clearly visible, and it may be seen that both pleural centres are contributing fibres which, passing to the mid-dorsal line, form the origin of the subintestinal nerve. It should be observed that some fibres from the last named pass directly into the roots of the two pallio-columellar nerves. In fig. 52 the origin of the subintestinal nerve is distinct, and both it and the origins of the two pallio-columellar nerves appear to be imbedded in a mass of ganglion-cells in which the limits of the right and left pleural and the subintestinal ganglia can be traced with the aid of a little exercise of the imagination.

From what precedes, it follows that the pleuro-pedal centres are extremely complicated and are largely composed of definite tracts of nerve-fibres, some commissural, some decussating, some passing into the nerves issuing from this region. It is noticeable that there are several connections of a complex kind between the pleural and pedal centres as well as between the right and left pleural centres and the right and left pedal cords, and that there are evidences of numerous nervous relays throughout the region illustrated. No doubt, on analysis, these apparently complicated nerve-tracts can be reduced to five groups: (1) the pedal commissure, containing both direct and decussating tracts of fibres; (2) the pleuro-pedal connectives; (3) the cerebro-pedal and cerebro-pleural connectives; (4) the pleural commissure, peculiar to the Neritidæ and Helicinidæ; (5) the subintestinal connectives, derived from both right and left pleurals. Thus, the paths of the nerve-tracts might be described as normal, and consistent with our knowledge of the usual connections between the chief nerve-centres of Molluscs; but a study of sections will show that the arrangements are not so simple as might be inferred from a superficial examination of the ganglia and their commissures and connectives. For example, it appears that the cerebro-pleural connectives contain fibres derived from the pedal centres and that all the principal nerves contain fibres derived from two or more areas in the fused pleural and pedal ganglion-mass. I have been unable to pursue the subject further at the present time, and it is difficult to make any further progress because of our ignorance of the physiology of the molluscan nervous system. The main nerve-trunks must contain both afferent and efferent nerves, and it seems evident that these pass to different areas of the cortical layer of ganglion-cells, but as at present we have no means of distinguishing between these two kinds of fibres further analysis of the details of the nervous system is impossible. It may be of use to future workers on this subject to remark that there are two kinds of ganglion-cells in the cortical layer: larger cells with clear nuclei staining faintly in hæmatoxylin, and much more numerous smaller cells with deeply staining nuclei. It should be possible to trace the connection of the nerve-fibres with these different kinds of cells, but such an investigation demands fresh material, and could form no part of the present work on the Helicinidæ.

As Bouvier found considerable differences in the size and shape of the cerebral ganglia in *Helicina sagraiana* and *H. brasiliensis*, I have studied these centres with care in the hope that I might discover characters of classificatory value, but I have been no more successful here than I was in the case of the genital ducts. The characters to which Bouvier draws special attention are the relative size of the cerebral ganglia (enormous in *H. brasiliensis*); the size and shape of the labial lobe; the origin of the labio-proboscidian nerves, which all spring from the labial lobe in *H. brasiliensis*, but only one has this origin in *H. sagraiana*. As regards

the relative size of the cerebral ganglia I find that the proportion of each cerebral ganglion to the pleuro-pedal mass is expressed by the following figures:—in *Alcadia palliata*, $\frac{1}{2}$; *Alcadia hollandi*, $+\frac{1}{2}$; *Eutrochatella pulchella*, $\frac{2}{3}$; *Lucidella aureola*, $\frac{3}{4}$; *Paleohelicina ide*, nearly $\frac{1}{2}$; *Orobophana pousonbyi*, $\frac{1}{5}$; *Aphanoconia gouldiana*, $+\frac{1}{2}$; *Aphanoconia rogersii*, $\frac{2}{3}$. The relative length of the cerebro-pedal and cerebro-pleural connectives varies greatly: they are longest in the two species of *Alcadia* and in *Paleohelicina ide*; of moderate length in *Orobophana*, *Aphanoconia*, and *Eutrochatella*; extremely short in *Lucidella aureola*. I have counted four labio-proboscidean nerves on each side with more or less certainty in all the species examined with the exception of *Aphanoconia rogersii*, in which there appear to be five. Of these, counting from above downwards, the first and third are invariably stout nerves which branch soon after their origin; the second and fourth are slender and only divide into branches at their extremities. The labial lobe in all the species at my disposal has the form of a rounded boss projecting inwards from the antero-inferior edge of the ganglion: the shape and relative size of this lobe differ somewhat in the various species, but the differences are too slight to express in words. Fig. 53 (Pl. XXXIX.), representing the left cerebral ganglion of *Paleohelicina ide*, and fig. 54, representing the same ganglion in *Alcadia palliata*, show the extremes of difference in shape observed by me, and, on the whole, the cerebral ganglia of the Polynesian species resemble those of *Paleohelicina*, those of the West-Indian species those of *Alcadia*. The cerebral ganglia of the Helicinidæ, wedged in as they are between the anterior end of the pharyngeal bulb and the walls of the head, are nearly flat, the labial lobe projecting inwards beneath the pharyngeal bulb. Because of their flatness they are very readily stained and mounted as transparent objects, and figs. 53 & 54 give some idea of the complexity of the nerve-tracts and centres within the ganglion. One may distinguish an ocular centre, which is large relatively to the size of the ocular nerve, a tentacular centre, small relatively to the size of the tentacular nerve, and a relatively smaller commissural centre. Each of the labio-proboscidean nerves has a more or less well-defined centre of its own, but the buccal and labial commissures have no distinct centres at their origin. There is, further, a median lobe which possibly serves as a relay for various nerve-tracts running into and around it. It is evident that the nerve-fibres of the cerebro-pleural connective make direct and intimate connection with the ocular and tentacular lobes, and that a stout band of fibres curves round from the root of the cerebro-pleural connective to the base of the labial lobe, receiving on its way an accession of fibres from the cerebro-pedal connective. This nerve-tract makes connections with the centres of origin of the buccal and labial commissures and the labio-proboscidean nerves, and a well-defined curved band of fibres sweeps round from the origin of the first labio-proboscidean nerve to enter the

cerebral commissure, the last named also having connections with the tentacular and median centres. Evidently, the cerebral ganglia have undergone a high degree of concentration and integration, but it is to be remarked that if the labial lobe as figured for *Alcadia* were pulled out towards the bottom of the picture, it would form an elongated labial process from which the labio-proboscidian nerves would be given off at intervals, as is the case in *Trochus* and *Turbo*. In other words, the labial lobe, as it seems to me, is represented, not solely by the little projecting boss from which the labial commissure originates, but by all that part of the ganglion that lies below a line drawn from the lower side of the origin of the cerebral commissure to a point just above the origin of the buccal commissure.

The buccal ganglia, with their commissures and the nerves originating from them, have been very correctly figured by Bouvier.

The organ which I have mentioned above as connected with a branch of the left opercular nerve is shown in section in fig. 55 (Pl. XL). It is deeply embedded in the muscular tissue of the opercular lobe and lies to the left of the anterior end of the lobe close to the origin of the left columellar muscle. It consists of a cartilaginous plate of subtriangular form, the edges of the anterior apex inrolled ventrally and eventually fused so as to form a short conical tube. This cartilage forms, as it were, the cover of a flattened sac (fig. 55, *sac.*) lined throughout by an epithelium which is thin and composed of a single layer of somewhat flattened cells on the side attached to the cartilaginous plate, but thick and composed of columnar cells bearing short stiff cilia on the opposite side. Anteriorly this is continued into the tube formed by the inrolled edges of the cartilaginous plate, and here the columnar ciliated cells form a nearly continuous lining to its cavity. Posteriorly, as shown in fig. 55, the ciliated cells forming the floor of the sac (the reader must understand that the figure is reversed, so that the ventral side is uppermost) rest on a thick basement-membrane, from which a broad band of muscular fibres spreads to be attached partly to the muscular wall of the left side of the neck, partly to the bands of muscular fibres passing over the otocysts. Into this muscular band the large branch of the left opercular nerve penetrates. Taking an anterior course this nerve gives off a branch to the opercular muscles, but its main trunk is directed towards the anterior tubular end of the organ under consideration, and there passes through a small perforation in the cartilaginous wall and is distributed to the ciliated columnar epithelium lining the cavity of the sac. Dorsally the cartilaginous plate is connected with the left columellar muscle by a stout muscular band passing obliquely outwards. Above this band are seen in fig. 55 the sections of two convolutions of a coiled glandular tube, which on the one hand communicates by a very narrow duct with the anterior tubular end of the above-mentioned sac, and on the other hand opens to the exterior,

near the left anterior edge of the operculum, between it and the membranous flap that surrounds the opercular lobe. This tube is lined throughout by a glandular epithelium composed of rather tall goblet-cells with deeply staining basal nuclei and clear cell-contents.

If, now, we enquire into the morphological significance of this peculiar organ, I think there can be little doubt as to its homology. It occupies the same position and receives the same nerve-supply as the crypt into which fits the curved process of the operculum in the Neritidæ. This process is no longer to be seen on the operculum of the Helicinidæ, but from a study of the muscular attachments in the two groups I am inclined to think that the cartilaginous plate described above represents its inner extremity, all direct connection with the operculum being lost. In connection with it new structures have been formed, viz. the sac and the glandular tube. What its physiological significance is it is hard to say. It is clear that, by contraction of the muscular bands attached to it, the sac may be widely dilated, and when dilated, air must flow into it through the glandular tube. The abundant nerve-supply and the character of the columnar epithelium bearing short stiff cilia suggest that the sac has a sensory function, and it is possible that it may be a special sense-organ, likely enough of an olfactory character, which enables the animal to receive impressions from the external world when retracted into its shell. For the opening of the glandular tube is in such a position that it would open to the outer air whenever the opercular plug was ever so little loosened.

The pedal gland, an organ which is absent in the aquatic Neritidæ, is largely developed in the Helicinidæ. Its position and general structure are roughly indicated in fig. 45 (Pl. XXXVIII.). It consists of a main duct below the pleuro-pedal nerve-mass and extending some little way but not far back below and between the pedal cords. The duct is lined by a columnar ciliated epithelium raised on the ventral side into two prominent ridges, one on either side of the middle line. Surrounding the duct are bunches of unicellular glands, which penetrate among the interlacing muscle-fibres of this region of the foot. Each unicellular gland is prolonged into a fine duct which passes between the epithelial cells of the main duct and opens into its lumen. The histology of this gland is reminiscent of that of the byssus gland of lamellibranchiate molluscs, described by me in another place. The main duct opens at the anterior end of the foot, in the middle line, below the snout.

Mention may be made here of the large mucous gland which I agree with Thiele in identifying as the hypobranchial gland. It is of relatively enormous size in the Helicinidæ, but in structure and position does not differ much from what I have described for the Neritidæ. It opens into the mantle-cavity (Pl. XXXV. figs. 28 & 30) just in front of the aperture of the vaginal duct and, as shown in figs. 30 to 35, it forms a considerable glandular mass bulging

into the mantle-cavity to the left side of the genital ducts. As may be seen in figs. 16-20 (Pls. XXXII. & XXXIII.), it extends far beyond the hind end of the genital ducts, accompanying the rectum in its course, and lying to the right side of the kidney at the hinder extremity of the visceral mass. In the section depicted in fig. 20, which passes through the rectal coil at the bottom of the hind end of the visceral mass, the hypobranchial gland on the right side of the rectum appears to form a pair with the kidney on the left, but there is, of course, no relationship between the two organs. Throughout its course the hypobranchial gland consists of an irregularly folded flattened sac, from which short glandular diverticula are given off in all directions. In its terminal part, as is shown in figs. 18-20, the gland appears to be differentiated into two portions: one lying nearer the oesophageal end of the stomach is lined by an epithelium loaded with fine dark granules; the other portion, lying nearer to the mantle-cavity, is lined by an epithelium of the character shown in Pl. XXXIX. fig. 56. It is made up of large glandular cells, oblong in outline, and filled with a highly refracting granular substance which, when the cells are ready to discharge their contents, is accumulated into oval pellets, as shown in the figure. Between the gland-cells are long and very attenuated interstitial cells, of which the outer ends are expanded and produced to form a cover over the outer ends of the gland-cells. The nuclei of the interstitial cells lie in their expanded outer ends. I could find no trace of cilia. In nearly every specimen examined the mantle-cavity was full of a sticky gelatinous mass secreted by the hypobranchial gland.

From what precedes it is evident that the Helicinidæ are a very homogeneous group, so far as their anatomical characters are concerned, and that such differences as I have been able to detect are of very little assistance in classification, the resemblances and differences in one set of organs suggesting one class of affinities, those of another set of organs suggesting another class. Thus, taking the arrangement of the coils of the intestine as a criterion, we should place *Alcudia*, *Orobophana*, and *Paleohelicina* close together, with *Lucidella* related but somewhat apart: *Eutrochatella* would go with *Aphanoconia* to form a distinct group. But if we took the characters of the female gonaducts as a criterion we should get a different arrangement. *Eutrochatella* would stand nearest to *Alcudia*, with *Aphanoconia* more distantly related: *Paleohelicina* with *Orobophana* would form a distinct group.

The nervous system is so similar in all the species that it affords a very slight guide, but, as far as the cerebral ganglia give any clue, the genera would fall into an arrangement consistent with their geographical distribution; *Alcudia*, *Lucidella*, and *Eutrochatella* forming one group; *Paleohelicina*, *Orobophana*, and *Aphanoconia* another. Finally, the radular characters, which have attracted a considerable share of the attention of systematists and in my experience afford the most reliable and readily

recognizable marks of distinction between different species, give a totally different result. Taking these as a criterion, *Eutrochatella* stands well apart: the remaining genera show a sufficient amount of similarity to justify our placing them in a single group, in which *Palæohelicina* stands nearest to *Alcadia*; *Aphanoconia* is closely related to *Palæohelicina*; *Orobophana*, while showing relationship to the two last named, has distinctive characters which keep it somewhat apart; and *Lucidella*, while showing relationship to *Alcadia*, has undergone modifications which, in one feature at any rate, resemble those which distinguish *Orobophana* from *Palæohelicina*.

On the whole, the radular characters afford the safest clue to affinity, agreeing as they do with the conclusions founded on conchological characters and on geographical distribution.

In all the Helicinidæ, so far as is known, the radular formula may be represented as $\infty . 1(3+1+3) . 1 . \infty$. The Proserpinidæ have a somewhat different, and the Hydrocenidæ a very different, formula, but they need not be considered here.

As different authors use different names in describing the teeth of Neritoid gastropods, I must define my terms before proceeding further. Of the teeth included in brackets in the formula, I call the single tooth in the centre the *median*; the three teeth on either side of it the *admedians*. The large tooth on either side of the admedians I call the *lateral*, and the numerous teeth to the outside of these the *marginals*. In *Eutrochatella*, as Troschel has shown, the lateral teeth are relatively very large and of characteristic shape, being mushroom-shaped, with the top of the pileus hollowed out to form an articular cavity, into which fits the stalk of the lateral tooth of the row next in front of it. The edge of the pileus is entire. I have attempted in fig. 57 (Pl. XL.) to give some idea of the very complicated structure of this tooth in *Eutrochatella pulchella*. It should be noted that it has an external process, or "Basalanhang," which Troschel described as characteristic of the genus *Helicina*. For the rest, this mushroom-shaped tooth more nearly resembles in shape the corresponding radular tooth in the Neritidæ than is the case in any other Helicinid. The marginal teeth of *Eutrochatella* are simply pointed curved bars, without denticulations at their free extremities. In the genus *Helicina* Lamarck (*non sensu restricto* Wagner) the laterals are not pileiform, but consist of a stout median portion which I shall call the "stalk"; from the inner side of this a more or less broad aliform plate projects obliquely forward; the anterior border of this plate is thickened, recurved, and bears a number of denticulations, varying from 7 to 12 in number in the different species that I have studied. Attached to the outside of the stalk by an imperfect joint is the pointed external process (the "Basalanhang" of Troschel), and the top of the stalk is excavated to form an articular cavity for the hinder end of the stalk of the corresponding tooth in the row next preceding. Also, in all species of *Helicina* the marginal teeth have broadened recurved

anterior extremities bearing denticulations. Thus, there is a considerable difference between *Eutrochatella* and *Helicina*, but the gap is bridged over by *Trochatella chrysochasma*, in which, according to Troschel, the lateral tooth is pileiform, but with an oblique anterior border bearing from 7 to 9 denticulations, and whereas the proximal marginal teeth are simply pointed as in *Eutrochatella*, the more distal marginals bear denticulations, increasing from one to four in number. I have shown that anatomically *Eutrochatella* bears the closest resemblance to *Alcadia*, differing only in the arrangement of the coils of the intestine.

The genus *Alcadia* is characterized by a notch separating the peristome of the shell from the columella. It is stated (Fischer, 'Manuel de Conchyliologie,' p. 795) that the operculum has a dentiform process: I can only say that I cannot find a trace of any such structure in *A. palliata* and *A. hollandi*. In all other respects *Alcadia* is similar to the point of identity to *Helicina*. Troschel declares that the only recognizable difference between the radulæ of *Alcadia* and *Helicina* is in the form of the median tooth, a character of very little value, for, as I shall show, the shape of this tooth varies from species to species. But Troschel's figure of the radula of *Alcadia* is not very exact. I have given in Pl. XL. fig. 58, *a* to *f*, large scale drawings of the teeth of *A. hollandi*; those of *A. palliata* differ only in minute particulars. Comparing these with the drawings of the radulæ of *Lucidella*, *Palæohelicina*, *Orobophana*, and *Aphanoconia* (Pls. XL.-XLII. figs. 59-65), it will be seen that the first admedian tooth of *Alcadia* has a characteristic shape, being subquadrangular in outline, with its anterior outer angle produced into a knob on which are borne four blunt denticulations. The large lateral has a short stalk, hardly projecting behind the origin of the aliform plate: the latter is large, expanded, bearing seven stout but blunt teeth on its recurved anterior margin. The articular excavation is very shallow: the external process long and pointed.

Of the other radulæ figured, those of *Palæohelicina* (Pl. XLI. fig. 60) and *Aphanoconia* (Pls. XLI. & XLII. figs. 62-65) bear the closest resemblance to *Alcadia*. Both these genera were included in *Helicina* Lamarck, and have only recently been separated by Wagner. In them the lateral teeth have the same general shape as in *Alcadia*, but the stalk is longer, the aliform plate less expanded, the denticulations on its anterior border vary in size, shape, and number. The first admedian tooth is very similar in the two genera, and differs from that of *Alcadia*. The median tooth is very variable in size and shape. The similarity of the radulæ of *Palæohelicina* and *Aphanoconia* is remarkable, and leads one to doubt whether Wagner is justified in placing these forms in different genera. On the other hand, *Orobophana* (Pl. XLI. fig. 61) is distinct: its lateral tooth is that of *Palæohelicina*, but the first admedian is relatively large, acutely triangular, its anterior border thickened but without denticulations; it is feebly corneous and nearly transparent, suggesting that it is in

course of disappearance. The median tooth is heart-shaped, minute, and similarly feebly corneous. *Lucidella* (Pl. XL fig. 59) is quite distinct in radular characters: in the lateral teeth the stalk is practically obsolete, the bulk of the tooth consisting mostly of the aliform process with its thickened denticulate border, which is continued posteriorly into the articular knob. There is no anterior articular excavation, but a thin triangular external piece which serves to support the articular knob of the tooth of the row next in front, and for the attachment of the external process. The third admedians are of the usual petaloid shape; the second admedians stout, triangular, with a thickened curved anterior edge, bearing on its outer surface a small minutely denticulate trenchant process. The first admedians are rather large, but feebly corneous, with a thickened anterior non-denticulate border; they have been modified in a manner analogous to what has been observed in *Orobophana*. The medians are broadly heart-shaped, feebly corneous, nearly divided into two by a deep median anterior notch.

Summing up these details and taking into comparison Troschel's figures, which are mostly of species of *Helicina* sensu restricto of Wagner, and confining our attention to the lateral tooth, which is the largest and obviously of most functional importance in the Neritacea as well as in the Helinacea, we see that there is an easy transition from *Eutrochatella* to *Alcadia*: that the lateral tooth of *Alcadia* is of the form characteristic of the Helicinidæ in general, but shows a tendency to a reduction of the stalk, which, as Troschel has shown, is common to many American and West-Indian species. This tendency is exhibited in an extreme form by *Lucidella*. But in the Pacific and Oriental genera the stalk and the articular excavation connected with it are well developed. But the lateral tooth of *Eutrochatella* bears an extremely close resemblance to that of the Neritidæ, and there is this further resemblance, that the first admedian tooth, which is of very large size in the Neritidæ, is relatively of much larger size as compared with the second and third admedians in *Eutrochatella* than in any other Helicinid. If such characters can be relied upon as a guide to affinity, *Eutrochatella* is the most closely related among the Helicinidæ to the Neritoid ancestor of the group. From *Eutrochatella* forms have been derived: on the one hand, the Proserpinidæ, which also have a large pileiform lateral tooth; on the other hand, *Helicina*. We may infer that the earliest *Helicina* retained the stalk and articular excavation which are such marked features in the pileiform lateral tooth of *Eutrochatella* and *Proserpina*.

The forms which, as suggested in the earlier part of this paper, were transported by some unknown means across the Pacific Ocean to the Philippines must have possessed these features and transmitted them unchanged to their descendants which now inhabit the Oriental and Indo-Pacific regions. But in America and the West Indies there has been a tendency, more

fully realised in some species than in others, to a reduction of the stalk and articular cavity, this reduction being shown to a slight degree in *Alcadia*, to a marked degree in *Lucidella*.

In all the Helicinidæ there is a tendency to the reduction of the central and admedian teeth: this tendency is shown in a marked degree in *Lucidella* and *Orobophana*, but must have reached its present degree independently in these two genera. The reduction is carried to an extreme degree in *Hydrocena*, in which the second and third admedians have disappeared; the median and first admedian are present, but in a rudimentary condition, and the laterals are reduced to mere rods of no great size. But I am disposed to think that the Hydrocenidæ must have branched off from the Neritoid stock independently of the Helicinidæ. They retain many primitive features, as Thiele has shown, among others the process of the operculum which is quite Neritoid in character, and their geographical distribution favours this view. *Hydrocena* is confined to the marine littoral of Dalmatia; *Georissa* lives at considerable altitudes on the Khasi Hills in India. It is by no means improbable that pulmonate forms may have been developed more than once from such animals as the Neritidæ, which show a predilection for migrating as far as possible out of the water, and for the rest of it, the most that can be said in favour of uniting the Hydrocenidæ with the Helicinidæ is that both display strong Neritoid affinities.

The main result of my researches is to show that in such a limited group as the Helicinidæ the systematists are justified in their methods. The visceral anatomy of all the forms that I have examined is strikingly similar, and where deviations occur they are contradictory and of uncertain value. The Helicinidæ appear to have inherited an organization with marked Neritoid characteristics, and to have maintained it, with little or no change. Presumably that organization is well adapted to the somewhat narrow range of the conditions of their existence, and any deviation from it has been checked by the action of natural selection. But there are a thousand deviations, in all directions, among characters which cannot by any stretch of the imagination be claimed to be of any importance in the struggle for existence. Such characters are the texture and coloration of the shell; the shape of the aperture; the extent and distinctness of the basal callus; the presence or absence of folds at the aperture of the shell; the presence or absence of a minute notch, such as occurs in *Alcadia*; the arrangement of the growth-lines on the operculum. It might be said that the operculum is an important protective organ and therefore eminently susceptible to the action of natural selection. But its function is simply to close the aperture of the shell, and this it does equally efficiently in all the species that I have examined, the number of these being much larger than the few available for anatomical study. As long as the operculum performs this function efficiently minute characters, such as the greater or less distance of its nucleus from

the anterior border, cannot possibly determine the question of the death or survival of the animal. The same reasoning applies to the variations of the radular teeth: the function of the radula is to rasp, and any of the modifications shown in figs. 60 to 65 is equally efficient as a rasp. Nobody, I think, would venture to assert that the minute differences in the four species of *Aphanoconia* (figs. 62 to 65) could have had any value in the differentiation of these species by natural selection.

As a result of my somewhat elaborately minute studies, I am driven, and, I confess, somewhat unwillingly driven, to the conclusion arrived at by a number of naturalists, that natural selection is efficient in preserving characters of physiological importance, but ineffective in producing new species by adding together numerous minute successive variations. The only conclusion justified by the facts seems to me to be that the characters on which systematists rightly rely are of the nature of deviations or mutations, of no consequence to the well-being of the animals in which they appear, but inheritable, and therefore perpetuated under favourable circumstances by segregate breeding. The Helicinidæ, inhabiting narrow areas, and often segregated in remote islands, afford particularly favourable opportunities for segregate breeding.

As to how far these small deviations of functionally unimportant structures may be due to the influence of external conditions I do not venture to offer an opinion, but the following fact is suggestive. Among the shells in the tube containing several specimens of *Aphanoconia merguensis* was a specimen which in size, shape, coloration, and marking so exactly resembled the others that I took it for a Helicinid (as the collector must also have taken it) and decalcified it with a view to anatomical investigation. It proved to be a Helicid, of what genus and species I cannot say, as I had destroyed the shell and could not find another specimen.

Among the collection of Helicinidæ made in the Andaman Islands and presented to the British Museum of Natural History by Mr. G. Rogers was a tube containing half a dozen specimens which differ recognizably in the characters of the shell and operculum from *Aphanoconia andamanica* Benson, but are clearly closely related to that species. I have not been able to refer them to any named species, and as the radular characters show it to be distinct from *andamanica*, I describe it as a new species, as follows:—

APHANOCONIA ROGERSII, sp. n. (Pl. XLII. figs. 65-69.)

Shell oblatly spheroidal, the surface marked with closely set radial growth-lines; colour light orange-yellow marked with more or less distinct reddish-brown radial bands; spire of $4\frac{1}{4}$ whorls, increasing regularly and somewhat rapidly in size, the last whorl obtusely keeled, the keel produced into a prominent angular

projection at the peristome. Aperture semilunar, very oblique, the outer margin thickened and expanded. Basal callus not very thick, hardly differing in colour from the rest of the shell, of rather small extent, its limits clearly defined above, as well as below. The whole shell deeper in proportion to its breadth than in *A. andamanica* and the spire more prominent.

Operculum yellowish white in colour, the calcareous plate rather thin, the sigmoid curve pronounced, the upper angle produced.

Radula with small diamond-shaped median tooth; the first admedian tooth more than twice as long as broad, the anterior edge incurved and bearing four denticulations; second and third admedian teeth each with four denticulations; the lateral teeth normal, the stalk rather long, the articular excavation deep, the aliform process bearing seven round denticulations.

Closely as the shell of this species resembles that of *A. andamanica*, a glance at the drawings of the radulae of the two species (figs. 63 & 65) shows that they are distinct.

I must express my obligations to Miss Margaret Poole, both for helping me in the determination of the different species of *Aphanoconia* and for making the drawings of shells and radulae for figs. 62 to 68.

As I have discussed and offered an explanation of the geographical distribution of the Helicinidae without either adopting or criticizing the theories advanced by Dr. Simroth (7 and 8) on this subject, I must, in conclusion, make some reply to the friendly criticisms that he has published on my paper on the Neritidae. I do not propose, in this place, to discuss the physiological interpretation that he has given of the different arrangements of the female ducts in the Neritidae. For one thing, I have obtained some new material and hope soon to publish further observations throwing fresh light upon the problems to which he refers: for another, I am inclined to accept much of what he writes on that part of the subject.

But with regard to the ancestry of the Neritidae, and with them the Helicinidae, which Dr. Simroth would derive from a pulmonate stock, and with regard to the homologies that he wishes to establish between the generative ducts of Neritidae and Pulmonata, I am unable to accept any of his conclusions. To do so would be to throw the whole fabric of morphological reasoning to the ground. Dr. Simroth's views on homologies are largely influenced by a theory of secular changes in the sea-level produced by a swinging or "pendulating" movement of the earth about an axis which corresponds with the longest diameter of the earth and has its poles in Sumatra and Ecuador. It is not my present intention to discuss the difficult astronomical and geological problems involved in the "Pendulation theory," and, indeed, I am sure that I am incompetent to discuss them. The theory may be well founded or it may not: I do not offer an opinion; but be it right or

wrong, I fail to see that the conclusions deduced from it by Dr. Simroth are necessary. I will explain as briefly as possible why. Unless I misunderstand him grievously, and if I do I beg his pardon, one of Dr. Simroth's chief conclusions is that, contrary to the generally accepted doctrine, marine and freshwater animals in general, the marine prosobranch Gastropods in particular, are evolved from terrestrial forms which have been forced by the above-mentioned secular inundations to adapt themselves to new conditions of life and make their habitat in another medium. As the pendulation theory applies to all geological time, if the precursors of marine Gastropods were terrestrial in habit, we should find evidence of this in geological deposits. The earliest-known Gastropods, from the Cambrian to the Devonian, would bear evidence of their terrestrial life, those found in later deposits would indicate, in some periods at least, the change from a terrestrial to a marine existence. But, in point of fact, the geological evidence points decisively the other way. In Cambrian, Ordovician, Silurian, and Devonian deposits we get Gastropods belonging almost exclusively to the Streptoneurous Aspidobranchia and Pectinibranchia. There are, it is true, the pteropod-like shells of the Conularida which, if they are really remains of Pteropods, would demonstrate the great antiquity of highly specialized forms of Euthyneura. But the true systematic position of the Conularida is at the best doubtful, and it has been urged with much reason and on high authority that the resemblance between the shells of these archaic forms and the more modern Pteropoda is due to parallelism. As so much doubt prevails as to their affinities, the Conularida cannot be brought into the argument. The Aspidobranchiate and Pectinibranchiate Gastropods from these earlier Palæozoic deposits are without doubt marine forms. They subsisted, without any important changes, through the four above-mentioned geological epochs, and one genus, *Pleurotomaria*, has survived to the present day. We know the habits and the anatomy of *Pleurotomaria*, and they support in a most remarkable manner the conclusions derived from an extensive knowledge of gastropod morphology. On the other hand, with the exception of *Hercynella* from the Devonian, undoubted Euthyneura first make their appearance in the Carboniferous. They belong to the Actæonidæ and Pulmonata Stylommatophora. The first-named family is marine, and anatomically displays so many streptoneurous characters that it might almost be included in the Aspidobranchia. Of the Stylommatophora we get forms like *Dendropupa* and *Pyramidula*, unquestionably terrestrial species, and, according to views generally accepted, highly modified and therefore indicative of a line of lost ancestry probably allied to the contemporary Actæonidæ. But these pulmonate forms are few and of rare occurrence in the Carboniferous, a period in which the conditions for the preservation of terrestrial and freshwater forms were particularly favourable. Had numerous Pulmonates existed at that time their remains must have been more abundantly

preserved. Terrestrial pulmonates are still scanty in the Permian and Trias, and only begin to show a considerable increase in the Jurassic and Cretaceous. I need not labour the point further. Clearly, palaeontological evidence does not favour Dr. Simroth's theory of the origin of marine from terrestrial Gastropoda.

But let us suppose that palaeontological evidence may be ignored on account of the imperfection of the geological record, and that the Pendulation theory is so well supported by other evidence as to compel us to give credence to Dr. Simroth's doctrines as to the origin of marine from terrestrial Gastropods. The Helicinidae are terrestrial and pulmonate. I have shown, and in so doing have only corroborated the opinion of all other observers, that they are Neritoid in almost every feature of their anatomy. If the marine and fluviatile Neritids were to be derived from a terrestrial and pulmonate form, one would suppose that that form must have been Helicinid in character, for the affinities between the two groups are so very obvious. But Dr. Simroth does not discuss this possibility. Making reference to *Ostracolethe*, *Hyalimax*, *Limax*, and *Arion*, all highly specialized recent Pulmonates, he boldly derives the Neritidae from the Stylommatophora, relying largely upon the supposed homology of their generative ducts. This homology I do not admit: a resemblance there is, but not a close one, and, even if it were closer than it actually is, I should place very little reliance on the anatomy of the generative ducts as indicative of relationship between groups differing widely in all other respects. In the different phyla of invertebrated animals the generative ducts are notoriously variable in character. In the Platyhelminia, for example, their variety is bewildering. Within the phylum Mollusca there are many instances of variability and also of deviations which must have been independently acquired but are in the same direction, as, for instance, in the Doridomorpha and Elysionomorpha. The resemblances, such as they are, between the generative ducts of the monœcious Pulmonata and the diœcious Neritidae are just what one might expect to find in animals in which a common plan of organization, to wit a gastropod organization, is modified in accordance with similar physiological requirements. The differences are of amply sufficient magnitude to betray a difference of origin. In other words, the complex gonoaducts of Neritidae and Pulmonata are independently acquired structures, and such resemblances as they display are due to parallelism.

I have already referred to the anatomy of the Pleurotomariidae, a family which existed in the Cambrian and survives to the present day. Thanks to Bouvier and M. F. Woodward, we are well acquainted with the anatomy of *Pleurotomaria*, which affords a striking confirmation of the reliability of sound morphological reasoning. Before *Pleurotomaria* had been studied, comparative anatomists, as the result of extensive investigations of gastropod structure, had come to an agreement concerning numerous marks of primitive organization in the group. When this survivor from

the Palæozoic age came to be examined, all these marks were found, some of them in a more pronounced degree than in any other known Gastropod, and in no system of organs were these marks more conspicuous than in the nervous system, the importance of which Dr. Simroth seeks to minimize. Among these marks may be enumerated—a cerebral commissure situated far forward on the pharyngeal bulb; a distinct labial commissure; elongated and scalariform pedal nerve-centres; a long crossed visceral commissure; two auricles to the heart; the ventricle lapped round the rectum; a rhipidoglossate dentition. Other characters might be enumerated, but these suffice for the present purpose. All these characters are absent in the Pulmonata: all of them are present in the Neritidæ. Moreover, by discovering the oviduco-coelomic funnel, I was able to demonstrate, beyond all reasonable doubt, the homology of a part of the gonaducts to the right kidney of *Pleurotomaria* and other rhipidoglossate Aspidobranchs, a homology which Thiele had already asserted on other grounds. Now it is quite clear that, if structural resemblance is of any value as a guide to affinity, we have a choice between two alternatives. Either the Neritidæ, to which we must add the Helicinidæ, are descended from Aspidobranch ancestors, which they resemble in all the points enumerated above, and have independently acquired genital ducts superficially similar to those of Pulmonata; or, as Dr. Simroth will have it, they have descended from stylommatophorous Pulmonata, have preserved the characters of the genital ducts of the latter group, but have independently acquired all the other characters enumerated above, characters possessed by no Pulmonate, but invariably present in those Aspidobranchs from which, on Dr. Simroth's showing, the Neritidæ are not descended. I am not quite sure whether he would go so far as to assert that the remaining Aspidobranchs possess those characters because they are descended from the Neritidæ. To make such an assertion would, indeed, be flying in the face of all reasoned opinion on this subject, and would amount to a declaration that the geologically more recent Pulmonates are the parents of their predecessors of Cambrian age!

I submit the alternative to the judgment of my readers, and in doing so beg leave to enter a protest against the growing tendency to throw over long-established and carefully reasoned conclusions founded upon morphological evidence, because of their unconformity with some new and as yet insufficiently tested hypothesis, or because they do not help in the solution of certain limited problems. I was quite aware, when I discussed the subject, that the geographical distribution of the Neritidæ was a puzzle, and that I had failed to find a solution to it. The distribution of the Helicinidæ is scarcely less puzzling and awaits a final solution. But with all respect for Dr. Simroth's authority and deserved reputation as a zoologist, I submit that the solution that he offers is improbable, raises a crop of other puzzles, and throws morphology into confusion.

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- (A complete list of the literature of the Neritoidea is given in my previous paper [2]).

EXPLANATION OF THE PLATES.

PLATES XXX.–XLII.

Lettering in all the figures.

<i>an.</i> Anus.	<i>con. ped.</i> Cerebro-pedal connective.
<i>ao.</i> Aorta.	<i>con. pl.</i> Cerebro-pleural connective.
<i>ap. mg.</i> Aperture of hypobranchial gland.	<i>c. ph.</i> Lateral pharyngeal cartilage.
<i>Au.</i> Auricle.	<i>div.</i> Diverticulum of male gonaduct.
<i>buc.</i> Buccal cavity.	<i>E.</i> Eye.
<i>cæ.</i> Cæcum of ootype.	<i>F.</i> Foot.
<i>cl.</i> Cloaca.	<i>g. bucc.</i> Buccal ganglion.
<i>c. m. l.</i> Left columellar muscle.	<i>g. cer.</i> Cerebral ganglion.
<i>c. m. r.</i> Right columellar muscle.	<i>Gd.</i> Gonaduct.
<i>com. bucc.</i> Buccal commissure.	<i>gl. pd.</i> Pedal gland.
<i>com. cer.</i> Cerebral commissure.	<i>gl. r.</i> Glandular ridge on floor of the œsophagus.
<i>com. lab.</i> Labial commissure.	<i>g. pl.</i> Pleural ganglion.
<i>com. pd.</i> Pedal commissure.	<i>Int.</i> Intestine.
<i>com. pl.</i> Pleural commissure.	

- Li.* Liver.
li. d. Liver-ducts.
M. Mantle.
M. c. Mantle-cavity.
m. g. Hypobranchial gland.
n. cm. l. Left columellar nerve.
n. cm. r. Right columellar nerve.
n. gen. Genital nerve.
n. gl. p. Nerve to pedal gland.
n. lpb. Labio-proboscidean nerves.
n. oc. Ocular nerve.
n. op. l. Left opercular nerve.
n. op. r. Right opercular nerve.
n. ot. Otocyst nerve.
n. pal.-c.l. Left pallio-columellar nerve.
n. pal.-c.r. Right pallio-columellar nerve.
n. pal.l. Left pallial nerve.
n. pal.r. Right pallial nerve.
n. par.l. Left parietal nerve.
n. par.r. Right parietal nerve.
n. sb.i. Subintestinal nerve.
n. ten. Tentacular nerve.
od. Oviduct.
od¹. Descending limb of V-shaped portion of oviduct.
od². Ascending limb of V-shaped portion of oviduct.
od. c. a. Anterior odontophoral cartilage.
od. c. p. Posterior odontophoral cartilage.
œ. Œsophagus.
œ. p. Œsophageal pouch.
o. œ. p. Opening of Œsophageal pouch into Œsophagus.
- oot.* Ootype.
Op. Operculum.
ot. Otocyst.
ov. Ovary.
Pc. Pericardium.
ped. Pedal nerve-cords.
ph. Pharynx.
R. Rectum.
rd. Radula.
rd. s. Radular sac.
r. p.c. Reno-pericardial canal.
r. s. Receptaculum seminis.
s. gl. Salivary gland.
Sn. Snout.
sp. d. Sperma-duct.
spz. Spermatozoa.
St. Œsophageal moiety of stomach.
St¹. Pyloric moiety of stomach.
t. Tentacle.
t. s. Terminal sac of male gonaduct.
Ur. Ureter.
Ur.p. Uropore.
V. Ventricle of heart.
vag. Vagina.
vag. ap. Opening of vagina into mantle-cavity.
vg. s. Vaginal sac.
V.G¹. First visceral ganglion.
V.G². Second visceral ganglion.
v. pal. Pallial vein.
v. pst. Posterior pallial vein.
v. ren. Afferent renal vein.

- Fig. 1. Left side view of *Alcadia palliata*. The mantle has been cut through close to the left columellar muscle and turned back to expose the interior of the mantle-cavity, the pericardium has also been opened.
 Fig. 2. Dorsal view of the buccal cavity, pharynx, and anterior part of the Œsophagus of *Alcadia palliata*: the buccal cavity, pharynx, and part of the Œsophagus have been laid open; *gl.r.*, glandular ridge on the floor of the Œsophagus.
 Fig. 3. A dissection of the Œsophagus and pharynx of *Alcadia palliata*, seen from the left side.
 Fig. 4. A horizontal section through the pharynx and buccal cavity of *Alcadia hollandi*.
 Fig. 5. The odontophoral cartilages of *Alcadia palliata*, viewed from below.
 Fig. 6. The odontophoral cartilages of *Eutrochatella pulchella*, viewed from above.
 Fig. 7. A dissection of the stomach of *Alcadia palliata*, viewed from the ventral side.
 Fig. 8. A portion of the epithelium of the stomach of *Alcadia hollandi*, showing glandular and ciliated cells. \times about 960.
 Fig. 9. Part of a section through the prominent ridge in the stomach of *Alcadia hollandi*, \times about 600; *cu.*, the thick cuticle covering the ridge.
 Fig. 10. The alimentary tract of *Alcadia palliata*, showing the arrangement of the intestinal coils.
 Fig. 11. Alimentary tract of *Alcadia hollandi*.
 Fig. 12. Alimentary tract of *Palæohelicina idæ*.
 Fig. 13. Alimentary tract of *Orobophana ponsoubyi*.
 Fig. 14. Alimentary tract of *Lucidella aureola*.
 Fig. 15. Alimentary tract of *Eutrochatella pulchella*.
 Fig. 16. A horizontal section through the upper part of the visceral mass of *Alcadia hollandi*. Figs. 17 to 22 are drawn from the same series of sections.
 Fig. 17. A section somewhat lower down, showing the origin of the ureter, *Ur.*, from the kidney.

- Fig. 18. A section still more ventral than the above, showing the deepest part of the pericardium and its relation to the kidney.
- Fig. 19. A more ventral section passing through the reno-pericardial canal, *r.p.c.*
- Fig. 20. A similar section passing through the ventral part of the visceral mass.
- Fig. 21. Part of a section slightly ventral to that drawn in fig. 19, showing the uropore, *Ur.p.*, opening into the mantle-cavity.
- Fig. 22. A section through the reno-pericardial canal. Magnified about 600.
- Fig. 23. Part of a section passing through the uropore of *Lucidella aureola* and showing the character of the renal epithelium. $\times 960$.
- Fig. 24. A diagram reconstructed from the series of sections drawn in figs. 16 to 20, showing the relations of the kidney, ureter, stomach, pericardium, and mantle-cavity.
- Fig. 25. The genital ducts of *Alcacia hollandi* ♀. The lower half of the figure is drawn as it appears when viewed by transmitted light, the upper part as seen by reflected light. In this and in figs. 26-29, 40, and 41, the gonads are represented as seen from the ventral side, after the wall of the mantle-cavity has been cut through by a dorsal incision and the rectum and gonaducts turned over to the right side of the animal.
- Fig. 26. The genital ducts of *Eurochatella pulchella* ♀.
- Fig. 27. The genital ducts of *Aphanoconia merquiensis* ♀.
- Fig. 28. The genital ducts of *Palæohelicina idæ* ♀.
- Fig. 29. The genital ducts of *Orobophana ponsonbyi* ♀.
- Fig. 30. A longitudinal section through the genital ducts of *Alcacia hollandi* ♀, passing through the aperture of the hypobranchial gland.
- Fig. 31. A longitudinal section from the same series, showing the aperture of the vaginal duct.
- Fig. 32. Another section from the same series, showing the origin of the oviduct from the ovarian chamber.
- Fig. 33. Another section from the same series showing the connection of the vagina with the vaginal sac and ootype.
- Fig. 34. Another section from the same series showing the opening of the oviduct, *od.*, into the descending limb of the V-shaped tube, *od.*'
- Fig. 35. Another section from the same series showing the receptaculum seminis opening into the ascending limb of the V-shaped tube.
- Fig. 36. Glandular epithelium from the wall of the ootype of *Alcacia hollandi*.
- Fig. 37. Ciliated epithelium and spermatozoa from the receptaculum seminis of *Alcacia hollandi*.
- Fig. 38. A section through the oviduct of *Alcacia hollandi*. Highly magnified.
- Fig. 39. An epithelial ridge from the bilobed cæcum of the ootype of *Orobophana ponsonbyi*.
- Fig. 40. A view of the genital ducts of *Alcacia hollandi* ♂.
- Fig. 41. A similar view of the genital ducts of *Aphanoconia gouldiana* ♂.
- Fig. 42. A drawing made from a combination of several serial longitudinal sections through the genital ducts of *Eurochatella pulchella* ♂, showing the narrow diverticulum, *k.v.*, which may possibly represent the vagina of the female and therefore be the homologue of the right kidney-sac.
- Fig. 43. A dissection showing the pedal, pleural, and visceral nerve-centres in *Alcacia palliata*, with the principal nerves issuing from them. The cerebral ganglia have been removed. The dissection is made from the dorsal surface; the foot, as is usual in contracted specimens, is turned forward and lies in front of the head with the sole uppermost; the walls of the head and the mantle have been cut away, and the visceral mass has been dissected as far as is necessary to show the course of the subintestinal nerve and its branches.
- Fig. 44. The nerve-centres and principal nerve-trunks of *Alcacia hollandi*, viewed from the right and above. The drawing was made with the camera lucida, after removal of the nerve-centres from the body.
- Figs. 45-52. A series of transverse sections through the pleuro-pedal nerve-centres of *Alcacia hollandi*, showing the principal tracts of nerve-fibres in the fused pedal, pleural, and subintestinal ganglia. For a full description of these figures, see the text, p. 789. The position of the pedal gland is indicated in fig. 45.
- Fig. 53. The left cerebral ganglion of *Palæohelicina idæ*, viewed from the inner surface. The ganglion is stained with Mayer's hæmalum and drawn by transmitted light; 1, 2, 3, 4, the four labio-proboscidian nerves.
- Fig. 54. A similar preparation of the left cerebral ganglion of *Alcacia palliata*.

- Fig. 55. A drawing of a section showing the position, structure, and nerve-supply of the opercular organ of *Eutrochatella pulchella*.
- Fig. 56. A portion of the epithelium of the hypobranchial gland of *Alcedia hollandi*. Highly magnified.
- Fig. 57. A left lateral tooth from the radula of *Eutrochatella pulchella*. Highly magnified.
- Fig. 58. Radular teeth of *Alcedia hollandi*, highly magnified: *a*, median; *b*, *c*, *d*, first, second, and third admedians of the left side; *f*, one of the marginals or uncini; *e*, a lateral tooth of the right side showing the stalk, *stk.*, the aliform internal plate, *al.p.*, the articular excavation, *art.*, and the process, *ext.p.*
- Fig. 59. Three rows of teeth from the radula of *Lucidella aureola*. In this and the following figures only the proximal members of the marginals are indicated.
- Fig. 60. Two rows of teeth from the radula of *Palaeohelicina ide*.
- Fig. 61. Two rows of teeth from the radula of *Orobophana pachystoma ponsonbyi*.
- Fig. 62. Two rows of teeth from the radula of *Aphanoconia gouldiana*.
- Fig. 63. Two rows of teeth from the radula of *Aphanoconia andamanica*.
- Fig. 64. Two rows of teeth from the radula of *Aphanoconia merguensis*.
- Fig. 65. Two rows of teeth from the radula of *Aphanoconia rogersii*.
- Fig. 66. Shell of *Aphanoconia rogersii*.
- Fig. 67. Shell of the same species, showing the aperture.
- Fig. 68. Shell of the same species, viewed from above.
- Fig. 69. Operculum of *Aphanoconia rogersii*, viewed from the inner or ventral side.

36. On the Palatability of some British Insects, with Notes on the Significance of Mimetic Resemblances. By R. I. Pocock, F.R.S., F.L.S., F.Z.S., Superintendent of the Society's Gardens and Curator of Mammals. With Notes upon the Experiments. By Prof. E. B. POULTON, F.R.S., F.Z.S.

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INTRODUCTION.

At the request of Prof. E. B. Poulton, F.R.S., I undertook, in the summer of 1909 and again in that of 1910*, to make a series of experiments in the Zoological Gardens to test the palatability of various species of British Insects. Much of the material was sent to me by Dr. G. B. Longstaff from Morthoe in Devonshire. Some I received from Prof. Poulton himself or from friends of his. A few species I added on my own account; notably the stick insects and the ants, of which we had an abundant supply in the Insect House in the Gardens. Those that I supplied I identified myself. The rest were in all cases named by the senders. To the insects Dr. Longstaff added a number of slugs, which were identified, I understand, by Mrs. Longstaff.

Since the majority of the experiments were made with English Insects, it is regrettable that English, or at all events Palearctic birds, were, for the most part, unavailable for the tests. There were two reasons for this. In the first place, Palearctic insectivorous birds were not strongly represented in the Society's

* Records of a few experiments made in 1911 have been incorporated in the text.